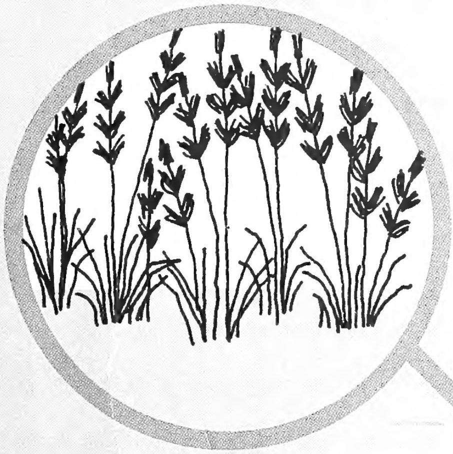

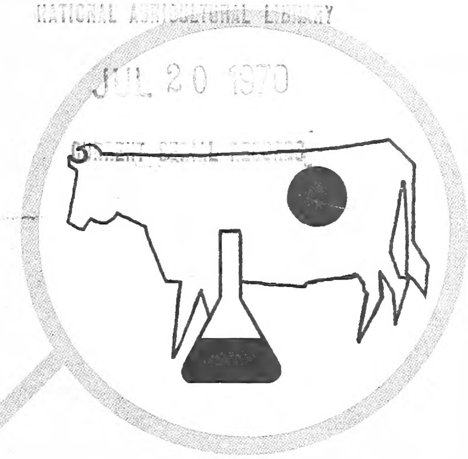

RANGE AND WILDLIFE HABITAT EVALUATION

A Research Symposium

U. S. DEPARTMENT OF AGRICULTURE / FOREST SERVICE / MISCELLANEOUS PUBLICATION NO. 1147

Range and Wildlife Habitat Evaluation– A Research Symposium

Range and Wildlife Habitat Evaluation—A Research Symposium

Sponsored by the Branch of Range and Wildlife Habitat Ecology and Management Research, Forest Service, U.S. Department of Agriculture

(Flagstaff and Tempe, Ariz. • May 1968)

MISCELLANEOUS PUBLICATION No. 1147
U.S. DEPARTMENT OF AGRICULTURE

MAY 1970
FOREST SERVICE

For sale by the Superintendent of Documents, U.S. Government Printing Office. Washington, D.C., 20402—Price $3

FOREWORD

Recent, rapid advancements in science and technology should encourage those responsible for proper husbandry and stewardsip of the Nation's nearly 1 billion acres of range and wildlife habitat resource. There is considerable knowledge of both the physical and biological processes governing the many range environments. New guides which are essential for wise management are being developed.

From time to time, Forest Service scientists have discussed, in national workshops, current information pertinent to a broad topic that is within their area of responsibility. Such meetings provide opportunities for Forest Service scientists to become more fully aware of recent technology and new scientific knowledge.

The first workshop in range and wildlife habitat research and management was held 30 years ago to consider planning, preparation, and publication of research results. A second was concerned with range seeding and noxious plant control. In 1962, a symposium on Range Research Methods explored vegetation measurement and sampling, measurement and evaluation of range use by livestock and game, and design and conduct of grazing experiments. Other regional conferences and meetings have enabled Forest Service personnel to review and update their philosophy and knowledge to meet their responsibility in range and habitat management in its broadest context.

The fourth conference, entitled "Range and Wildlife Habitat Evaluation—A Research Symposium," encompasses six sessions.

1. Forage evaluation for livestock and wildlife (four sessions).
2. Remote sensing in range and wildlife habitat evaluation.
3. Status, applications, and challenges of range and wildlife habitat ecology.

Scientists from the Forest Service and other Federal and State agencies and from universities contributed to the conference.

Note: It is the purpose of this publication to make available the papers presented at the conference to as extensive an audience as possible; except for editing, the individual papers are essentially as presented. Accordingly, the material represents the views of the individuals and not necessarily those of the Forest Service. Furthermore, reference to any equipment by trade name does not constitute endorsement of the product by the Forest Service, USDA.

HAROLD A. PAULSEN, JR.
ELBERT H. REID
Cochairmen

KENNETH W. PARKER, *Branch Chief of Range and Wildlife Habitat Ecology and Management Research*

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U.S. DEPARTMENT OF AGRICULTURE

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[1] Names and dates in parentheses refer to Literature Cited at the end of each article.

ANIMAL PRODUCTION AND FORAGE QUALITY

Definition and Components of Forage Quality

DONALD R. DIETZ[1]

The quantity of forage produced, measured by green or dry weight yield per acre, has long been the criterion of the value of a range for livestock, wildlife, or both. Only in recent years have the relationships between forage yield and quality and animal response been closely studied and partially understood (Sell et al. 1959). Several authors (Savage and Heller 1947; Cook and Harris 1950; Leopold 1950) have indicated that forage quality may be as important a factor as forage quantity in relation to animal carrying capacity.

Many of the terms used in forage quality studies will be defined in this paper, and some of the aspects and components of forage quality will be discussed. The discussion will be limited principally to forage quality as it relates to the ruminant animal on rangelands.

DEFINITION OF FORAGE QUALITY

Forage quality has been defined in many ways, but usually in relation to some animal response such as feed intake, weight gain, or production of milk or wool. Other terms associated with animal response, but which provide a measure of forage quality, are palatability, nutritive composition and digestibility, gross and digestible energy, and ruminal end products. Forage quality has also been estimated from such plant attributes as leaf-to-stem ratios and stages of plant maturity (Lucas 1963). Other indices of forage quality are: (1) Visual estimate of quality such as Federal hay grades, (2) leaf content of forage, and (3) botanical composition, particularly legume content (Reid et al. 1959).

Nearly all authors agree that high-quality forage for a ruminant animal will possess the following characteristics: (1) High palatability to the animal, with resultant high feed intake, (2) optimum levels of various nutrient components in proper ratios during period of animal use, (3) high apparent digestibility of the nutrient components with an optimum ratio of nitrogenous to nonnitrogenous components, (4) volatile fatty acids in optimum proportions for efficient energy production, (5) adequate levels of minerals, vitamins, and trace elements, and (6) efficient convertibility into components necessary for the animal body over sustained periods.

The range and wildlife scientist has several techniques available for evaluating forages on rangelands. Some of these are: (1) Chemical analyses, (2) animal feeding trials, (3) *in vitro* rumen techniques, and (4) grazing trials. The terms used in these techniques will be reviewed briefly.

DESCRIPTION AND IMPORTANCE OF NUTRITIONAL MEASUREMENTS

Chemical Constituents

Crude Protein

The term crude protein represents both protein and nonprotein nitrogen. It is calculated by multiplying the nitrogen percentage of feed by a factor, usually 6.25. True proteins are large, complex molecules composed of up to 22 amino acids. While it is true the test for crude protein does not indicate the kinds and amounts of amino acids present, no evidence indicates that ruminant animals require particular amino acids. Digestion in the rumen is a microbiological process, and amino acids are synthesized as needed (Sullivan 1962). Urea or other protein substitutes may equally well provide nitrogen for amino acid production.

Protein is considered the most important nutrient to the animal. A serious deficiency results in failure of the body to maintain itself, while even a slight deficiency adversely affects reproduction, lactation, growth, and fattening processes (Morrison 1957).

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Animals must have protein to form new cells essential for body maintenance, growth, reproduction, and lactation. The ruminant animal needs protein for the rumen micro-organisms to effectively digest and metabolize carbohydrates and fats. If protein levels fall below a minimum, rumen function becomes severely impaired. However, very high protein levels are not only unnecessary, but are inefficient for ruminant animals (Kleiber 1959).

Since crude protein content is significantly correlated to digestible protein content, determination of the crude protein level of a plant can give a reasonably reliable indication of its feeding value (Sullivan 1962).

Crude Fat

All of the various plant substances soluble in ether are included in the term crude fat. Lipids, plant pigments such as chlorophyll and carotene, and certain essential oils are removed from the plant in the ether extract (Maynard and Loosli 1956). Lipids contain true fats (reserve food material), waxes (cuticular components), and phospholipids (structural materials). The true fats are fatty acids esterified to form triglycerides (Bonner and Galston 1952). True fat provides approximately 2.25 times more energy than carbohydrates and proteins, but less than one-half of ether extract in plants may be true fat (Sullivan 1962). Some plants may contain quantities of volatile oils which have no feeding value and may be harmful to rumen micro-organisms, thus impairing rumen functions. The substances, called "essential oils" because of their odor or essence, give many plants their characteristic odor or taste. Big sagebrush (*Artemisia tridentata*), noted for its aroma, contains large amounts of essential oils (Nagy et al. 1964).

Ruminants are not dependent upon fat in the diet, because fatty acids can be synthesized in the rumen from carbohydrates and proteins. Dietary fat does, however, provide the most economical source of energy; thus, a deficiency causes the body to use a less efficient source of energy.

Carbohydrate

Three-fourths of the dry weight of plants is composed of carbohydrates, which include sugars, starch, cellulose, gums, and related substances. Thus, the bulk of the plant material eaten by range animals consists of some form of carbohydrate. Micro-organisms in the rumen break down the carbohydrate constituents and produce volatile fatty acids that provide most of the energy needed by the animal (Anninson and Lewis 1959). The carbohydrates considered in feed analyses are frequently presented as one or more of the following separate components:

Nitrogen-free extract (NFE).—The portion of the plant known as nitrogen-free extract contains most of the more soluble carbohydrates such as glucose, sucrose, maltose, and starch, and also some of the less soluble forms such as lignin, cellulose, and hemicellulose. There is no chemical test for this portion; it is calculated as the percentage of the sample remaining after the percentages of ash, crude fiber, crude fat, crude protein, and moisture are subtracted from 100. The disadvantages of this technique as it relates to forage quality are discussed under the section—"Chemical Analysis Systems."

Crude fiber.—The portion of the plant that withstands boiling in weak acids and alkalies is called crude fiber. Its resistant qualities are due to cellulose, hemicellulose, lignins, and other relatively indigestible constituents. Generally, high crude fiber content in forages indicates low digestibility by animals. However, ruminants are able to digest at least 50 percent of the crude fiber of most feeds. A certain amount of bulk, which is governed mainly by the crude fiber content, is thought necessary in the diet of animals to avoid the formation of a doughlike mass in the stomach (Maynard and Loosli 1956).

Lignin. —The complex, indigestible substances found in cobs, hulls, and the fibrous portions of roots, stems, and leaves are called lignin. Although the chemical structure remains uncertain all substances designated as lignin are considered to have a common basic structure (Maynard and Loosli 1956). Lignin has an important influence on the degree of digestibility of many feeds because the more lignified cellulose becomes, the less digestible it is to ruminants.

Cellulose. —Cellulose consists of a chain of glucose units called a polysaccharide. It is little affected by weak acids and alkalies, nor is it acted upon by enzymes secreted by the animal. It can be hydrolyzed by strong acids to form glucose. Rumen bacteria can break it down to form more soluble carbohydrates. It often combines with lignin as a framework for plants and for a protective coating of seeds. Cellulose is important nutritionally because it provides the body with a major source of energy. The digestibility of cellulose depends on its state of lignification (Sullivan 1962).

Hemicellulose.—Hemicellulose consists of a group of substances which are much less resistant to acids and alkalies than cellulose. They include polysaccharides such as the pentosans and certain hexosans that can be broken down into simple sugars and other products by the

enzymes of rumen micro-organisms. Hemicelluloses are widely distributed in forages, and are important because they contribute a major portion of the digestible carbohydrates in the animal diet (Maynard and Loosli 1956).

Ash

Almost all of the mineral content of plants is recovered in the ash left after ignition at 600° C. Thus, the presence of ash indicates the total mineral content, but does not indicate the individual minerals. It is often an advantage to know the ash content of forages because many measurements of digestibility and of certain substances which relate to digestibility are made on an ash-free basis (Sullivan 1962).

Calcium.—The ruminant animal must have access to adequate calcium. Calcium and phosphorus compounds are the most commonly analyzed minerals; they comprise about 90 percent of the mineral matter in the skeletons of livestock and about 75 percent of that in their entire bodies. One-half of the minerals in milk are calcium and phosphorus compounds (Morrison 1957). Calcium is also an important part of the blood plasma where it aids in blood clotting. On western ranges, calcium supplies are usually ample, and may be high enough to adversely affect the metabolism of phosphorus (Morrison 1957).

Phosphorus.—Phosphorus is vital in many body processes. It is an essential part of the skeleton, intracellular fluid, and compounds such as nucleoproteins and phospholipids. Phosphorus also is necessary in the transfer of energy (Anderson 1953).

Phosphorus is deficient in many forage species on western and southern ranges during the winter. Range livestock in these regions may need to be fed phosphorus supplements to maintain adequate phosphorus levels during late summer to early spring.

A deficiency of phosphorus or a wide calcium-phosphorus ratio may retard growth, create a high feed requirement, and cause an unthrifty appearance. A desirable calcium-phosphorus ratio is somewhere between 1:2 and 2:1, but ratios wider than 2:1 are permissible if sufficient vitamin D is present in the ration. A wide calcium-phosphorus ratio may prevent metabolism of phosphorus and thus result in a phosphorus deficiency (Maynard and Loosli 1956).

Other minerals.—Sodium, potassium, chlorine, magnesium, iron, sulfur, iodine, manganese, copper, cobalt, and zinc are necessary for many body processes. Some of these minerals function as constituents or activators of enzymes, and only very small amounts are needed. Many minerals, although important, are usually supplied in adequate amounts in common forage plants and are not normally reported in routine feed analyses.

Vitamins

Vitamins are organic compounds essential for normal functioning of the body. Their chemical role is largely catalytic: they usually form a part of or act with various enzymes, and only minute amounts are required (Peterson and Strong 1953). The oil-soluble vitamins —A, D, and E—cannot be synthesized by the animal body, but the water-soluble vitamins—C, B complex, etc.—can be synthesized from other food constituents by rumen bacteria.

Vitamin A and carotene.—Animals convert plant carotenes to vitamin A. While four carotenes in plants have vitamin A activity, only the beta form is a major source to the animal. Approximately 50 percent of the beta carotene in forage is converted to vitamin A by the animal body (Anderson 1953). Although vitamin A is needed in only minute amounts, animals can store it for only relatively short periods. A deficiency may develop after prolonged periods of feeding on forages devoid of green material. Unsuccessful reproduction, retarded growth, death of young, night blindness, eye lesions, and a general degeneration of the nervous system are symptoms of vitamin A deficiency (Morrison 1957).

Vitamin D.—The ruminant animal needs vitamin D, which is usually available in suncured forage or from the effect of direct sunlight upon the animal's body. When young animals are on green forage or when they receive too little sunlight, vitamin D deficiency may occur. Such a deficiency will cause rickets in young animals and will inhibit calcium and phosphorus metabolism in animals of all age classes (Maynard and Loosli 1956).

Vitamin E. —One of the oil-soluble vitamins, vitamin E (alpha tocopherol) is an important component of enzyme systems and is important in hormone production by the pituitary, adrenal, and thyroid glands. Adult animals rarely are affected by vitamin E deficiencies, because natural feedstuffs normally supply adequate quantities. Young animals, however, may suffer muscular dystrophy when on rations deficient in this vitamin. High levels of nitrites may result in vitamin E deficiencies. Vitamin E has antioxidant properties important in animal nutrition, since feeding vitamin E improves utilization of dietary vitamin A (Fruton and Simmonds 1953).

Energy

Energy is a highly significant measure of the nutritive value of feeds. Considerably more nutriment is required to maintain normal energy

metabolism than for all other purposes combined. Energy is the major basis in the compilation of diets for humans as well as of rations for livestock (Swift 1957).

With the possible exception of protein and phosphorus deficiencies, the most common nutritional deficiency affecting range animals is lack of either available energy, digestible energy, or both. Energy shortages may be due to insufficient feed, or to low dry-matter content in lush, watery feed. Even if abundantly available, low-quality roughage will not supply enough total digestible nutrients to meet the requirements of ruminants (The National Academy of Sciences-National Research Council 1957, 1963).

A shortage of energy-producing feed is most common on overused winter ranges and on early spring ranges at the time animals switch to watery green grass and forbs. Poor-quality winter forage adversely affects range animals in several ways: It provides insufficient energy; protein, and phosphorus may be inadequate for the animal to make efficient use of the available energy; and it causes cessation of growth, loss of weight, reproductive failure, and impaired rumen function. Also, range animals may eat an excessive quantity of watery green forage after spring growth begins. The result may be scours or inability of the weakened animal to adjust to the new feed, with consequent heavy mortality.

Gross energy is the heat given off by a substance during complete oxidation or burning. It is the starting point in determining the energy values of feeds. Energy is usually expressed in calories per unit of weight. A measure of gross energy is important because it provides a common basis for expressing nutritive value. In general, fats contain more than twice as much energy-producing substances as carbohydrates, while proteins have only slightly higher energy values than carbohydrates (Maynard and Loosli 1956).

Chemical Analysis Systems

There are several methods for separating plant material into various nutritive components. Some of these methods are discussed in this section.

Proximate Analysis

The method of proximate analysis was introduced prior to the 20th century, and is still in common use. It involves the determination of crude protein, crude fat (ether extract), crude fiber, ash by chemical tests and an estimation of nitrogen-free extract (by subtraction of the percentages of the other components from 100). The most obvious shortcomings of the proximate method are that crude fiber and nitrogen-free extract are not precise chemical groups, and that the carbohydrates are not necessarily separated into digestible and indigestible portions (Richards and Reid 1953).

The nitrogen-free extract portion does not have the high digestibility often attributed to it because it contains a large share of the lignin which is not digestible, and some of the cellulose which is partially digestible.

Despite the disadvantages of the nitrogen-free extract and crude fiber techniques for describing the carbohydrate portion of forages, the proximate scheme remains useful. Most of the literature in the animal nutrition field is based upon it. Until the methods of determining other carbohydrate components such as lignin and cellulose are adopted for routine analysis, the proximate method will remain in general use (Miller 1961).

Other Analysis Schemes

Many studies on the nutritional value of plants also present some data on mineral composition—usually, at least, percentages of calcium and phosphorus. Instead of crude fiber and nitrogen-free extract, some authors list percentages of individual carbohydrate components, including cellulose, hemicellulose, starch, reducing and total sugars, and lignin.

One of the newer methods to replace the crude fiber and nitrogen-free extract portion of the proximate scheme is to determine the lignin and cellulose content of forages. Many authors have found a highly significant negative correlation between lignin percentages and the digestibility of both dry matter and organic matter. There is a high negative correlation between lignin content and digestible energy, digestible cellulose, and digestible protein (Sullivan 1962).

The technique of Ellis et al. (1946) can be used to determine lignin and cellulose content. It is based on the insolubility of lignin and the solubility of cellulose in 72 percent sulfuric acid. This lignin method has several serious disadvantages: (1) Lignin is difficult to determine chemically, (2) its exact chemical structure is not known, and (3) routine tests for lignin are not standardized.

Van Soest (1966) proposes the determination of cell wall residues to replace the crude fiber technique. These residues can be considered chemical components of feedstuffs that cannot be completely digested. Cell wall constituents of plants can be separated into components that are: (1) Insoluble in a neutral detergent solution (attached protein), (2) soluble in an acid detergent solution (hemicellulose), and (3) insoluble in an acid detergent solution (lignin, lignified nitrogen compounds, keratin, and silica). The cell contents, such as lipids,

sugars, starch, nonprotein nitrogen, and soluble protein, are soluble in neutral detergent. Because this system separates the totally digestible, partially digestible, and indigestible portions of plants, it is much better than the crude fiber method.

Forage Digestibility

Although data on the proximate composition of plants indicate their probable nutritive value, feeding trials are needed to provide a more definitive reference (King and McClure 1944). Atwood (1948) reported that comparison of the gross composition of a plant to its ability to combat starvation shows a routine feed analysis alone is unreliable as an indicator of nutritive value, and that this analysis must be supplemented by digestion trials. Digestion trials have shown that older, more mature fall and winter forage is less readily digested than newer, tender spring growth; thus, any protein deficiency in the fall and winter may be much greater than that shown by routine chemical analysis (Biswell et al. 1945). Some of the measurements employed in digestibility studies are described in the following paragraphs.

The *in vivo* digestion trial is conducted (1) to record the amounts of feed consumed and the wastes excreted by an animal, (2) to determine the nutrient percentages of both feed and excreted substances by chemical analysis, and (3) to calculate the apparent digestibility of the individual nutrients. A 7-day conditioning period usually precedes a 7-day collection period; however, shorter intervals are sometimes used. Indicators are often used in conjunction with the digestion trial to facilitate the determination of feed intake and nutrient digestibility. *In vitro* digestion trials, using rumen liquor in artifical rumens to estimate forage digestibility, eliminate the need for handling large animals in digestion cages and feeding large amounts of forage.

Digestion Coefficient

The digestion coefficient of a nutrient is the percentage of a nutrient in a feed apparently digested by an animal. It is calculated from the amount of nutrients in the feed minus that recovered from the feces.

Digestible Protein (DP)

The percentage of protein in the ingested feed that remains in the animal body is called "digestible protein." It is listed separately in nutritional studies because of its importance in maintaining bodily functions.

Total Digestible Nutrients (TDN)

The term TDN indicates the sum of all digestible organic nutrients in a feed. The percentage of digestible fat is multiplied by a factor of 2.25 due to its higher energy value, and is added to the percentages of digestible protein, fiber, and nitrogen-free extract. TDN estimates the digestible energy value of the ration.

Nutritive Ratio (NR)

The ratio between the digestible protein and the sum of the digestible nonnitrogenous nutrients is called the nutritive ratio.

Digestible Energy (DE)

Digestible energy is calculated from the gross energy of feed minus the energy in the feces. It represents apparent digestibility, without correction for fecal constituents of metabolic origin. The digestible energy of feed is comparable to total digestible nutrients. Techniques are available for converting DE data to TDN (Morrison 1957). DE (and also TDN) is relatively unaffected by the plane of nutrition, environmental temperature, and physical activity of the animal. Many nutritionists consider DE one of the most practical and meaningful measurements of the nutritional value of a feed (Swift 1957).

Metabolizable Energy

The gross energy of a feed minus the energy lost in methane, urine, and feces is called metabolizable energy. It is more difficult to obtain than digestible energy and more subject to experimental error (Swift 1957).

Net Energy

The net energy of a feed is the gross energy minus the energy lost in feces, urine, methane, and in heat production. Theoretically, it is the ideal measurement of the nutritional value of a feed because it is the energy available to the animal for growth, maintenance, fattening, and other processes and activities. Actually, it is expensive and difficult to determine because of the need for exacting control over experimental procedures and conditions. Also, its applicability is limited because the results determined in the laboratory under carefully controlled conditions are not equally applicable to farm and ranch conditions (Swift 1957). Net energy values are subject to the limitations that the heat increment per unit of food intake varies according to the balance of the nutrients in the ration, the level of intake, the productive function, the species, and other factors. Thus, net energy values of feed cannot be considered constant (Maynard and Loosli 1956).

Because of its great potential importance in the field of animal nutrition, future research will undoubtedly be directed toward simplifying and standardizing net energy techniques.

It is important to remember, when consider-

ing the net energy of feed components, that the net energy values of protein, fats, and carbohydrates are different. True fat has the highest net energy value—more than twice that of protein and carbohydrates. Protein has much higher gross energy than carbohydrates, but due to greater metabolic losses in the animal, protein has about the same net energy value Energy is normally supplied by carbohydrates and fats in the diet, and body protein is utilized for energy only when the food supply is inadequate (Maynard and Loosli 1956). Protein yields its full value only when used for the building or repair of protein tissue or products (Morrison 1957).

Other Nutritional Measurements

Other methods are often employed to gain nutritional information about forages. Many are less laborious than the classic digestion trial or *in vivo* technique.

Nitrogen Balance

A nitrogen balance trial is similar to the digestion trial; however, urine and other nitrogenous products are collected and analyzed for their nitrogen content. The protein intake in the feed is compared to the protein loss in excreta, milk, and other sources. The balance trial provides a quantitative measure of protein metabolism and indicates whether the body is gaining or loosing protein. When nitrogen intake equals nitrogen loss, the animal is said to be in nitrogen balance or equilibrium, and is maintaining body condition. A continuing nitrogen loss—as animals may show on an inadequate diet—indicates the need for protein supplements (Maynard and Loosli 1956).

Nitrogen-Carbon Balance

A carbon balance is determined in addition to the nitrogen balance to provide more data on the gain or loss of fat. The carbon and nitrogen content of food, feces, and excreta, and carbon in the gaseous output of the animal are determined. The amount of carbon gained as protein is calculated and subtracted from the total carbon gained; the figure obtained indicates fat gain because almost the entire carbon content of the body is contained in protein and fat (Maynard and Loosli 1956).

Replacement Equivalents

The theory that two feeds are of equal quality when they result in the same weight gain, milk yield, etc. in animals, has been proposed for many years. This theory is the basis for Kellner's starch values and for Scandinavian Feed Units.

Kellner's starch values, a commonly used determinant in Europe, are calculated from information gained from nitrogen-carbon balance trials plus additional data on the fat-producing value of a feed. The fat-producing value is expressed as the number of kilograms of starch required to produce the same amount of fat as 100 kilograms of the feed. This use of a reference substance instead of the abstract measurement of calories provides a decided advantage in evaluating feeds (Kleiber 1959).

Scandinavian Feed Units are based on replacement trials with two groups of six or more cows. Barley is used as a reference standard in the ration of one group, while the feed to be tested replaces barley in the other ration. Milk production and body weight is maintained at the same level in both groups. The amount of test feed which maintains the same milk and body weight production as barley is said to be the equivalent as a feed (Kleiber 1959).

The limitation of the replacement equivalent methods is that protein requirements for body repair and growth are not considered. Kleiber (1959) comments "For milk production and growth, however, protein is a source of amino acids: It is not a fuel—it cannot be replaced by carbohydrates or fat." For this reason animals should be assured of an adequate protein level for their physiological activities and for their energy requirements.

Indicator Methods

Indicators have been used extensively for determining the digestibilities of feed. Internal indicators which occur naturally in the plant are lignin, plant chromogens, and nitrogen. External indicators which are added to the feed include chromic oxide, iron oxide, and monastral blue (Harris et al. 1959). The ideal indicator or marker will be totally indigestible and unabsorbable, have no action on the digestive tract, pass through the tract at a uniform rate, and be easily determined by chemical tests.

Determining the ratio of the indicator concentration to that of a given nutrient in both the feed and in the resultant feces permits calculation of the digestibility of the nutrient: measuring food intake or feces output is unnecessary (Maynard and Loosli 1956).

Nutrient Requirement Studies

After the nutritive content of a forage species is determined and its digestibility measured, the levels of each nutrient needed to meet the demands for growth, fattening, reproduction, and general maintenance must still be specified. Nutritional requirements of animals can be determined by feeding known amounts of individual nutrients at different concentrations, and measuring weight gain, body size, skeletal formation, reproductive ability, and milk production.

Other Forage Quality Indices

Forage Palatability

Palatability is that quality in a forage plant that makes it preferred when a choice between plants is available. It has been defined as the relative relish with which forage plants are consumed (National Academy of Sciences-National Research Council 1962).

The production of grazing animals largely depends upon (1) the amount of forage ingested and (2) the level of individual nutrients. Palatability may be equal to, or more important than, nutrient content because it directly influences the rate and total intake of forage (Hurd and Blaser 1962).

Palatability varies with species, location of animals, and previous experience, and it is influenced by the interrelationships of plant, animal, and environmental factors. Some studies have established that animals generally select forage high in important nutrients (Swift 1948), whereas other studies have shown correlations ranging from zero to high (Hurd and Blaser 1962). It is generally agreed, however, that plants high in sugar content are eagerly sought by ruminants.

Regardless of the relations between the palatability of forage and its nutritional value, any evaluation of the overall quality of a plant should include relative palatability because of its important effect on forage intake.

Other Forage Attributes

There are many attributes of plants that have been used to estimate forage quality. Some of the more useful ones are:

Federal hay grades. —The U.S. Department of Agriculture has formulated a grading system for hay based upon visual estimates of odor, color, leafiness, stem texture, and amount of foreign matter. The hay grades generally reflect the responses of growing cattle and milking cows to various qualities of hay. The hay grades are not precise enough, however, to accurately predict the feeding value of forage grown on a given farm (Reid et al. 1959).

Leaf content.—The leafiness of a forage is usually highly correlated with its nutritive value, because the leaves generally contain higher levels of important nutrients than the stems. Plant leaves contain more protein, phosphorus, calcium, and carotene, while the stems contain more fiber (Dietz et al. 1958). A wide leaf-to-stem ratio would indicate higher nutritive value than a narrow ratio (Reid et al. 1959).

Botanical composition. —Forage quality can be measurably influenced by the different proportions of the various plant species ingested by animals on the range. The use of forage legumes has been widely advocated, and has led to the inference that the nutritive qualities of legumes are superior to those of nonlegumes. There is evidence, however, that grass forage with an adequate protein content may produce animal responses (body weight gain, milk yield, etc.) equal to those from grass and legume mixtures because the energy production of the two sources may be approximately the same. In some situations, inadequate levels of protein and certain minerals in grasses could result in reduced animal response (Reid et al. 1959).

DISCUSSION AND SUMMARY

A review of the literature on forage quality provides the impression that, after a slow, faltering start, rapid progress is now being made. Almost all advances in both human and animal nutrition have been made in the past 50 years. Even with our increased knowledge, many problems associated with the concept of forage quality must still be solved. It is doubtful whether all the essential nutrient components for any species have been discovered (Maynard and Loosli 1956).

Many nutritional terms and tests, as well as other indices of forage quality, have been described in this paper. Which of these are most practical for the range technician to consider in evaluation of forage for livestock and wildlife? The proximate scheme of analysis, while useful, should be superseded by the newer techniques because of inherent weaknesses in describing the carbohydrate portion. For ruminant animals the following variables are recommended for consideration in routine analyses: Dry matter, gross energy, crude protein, fiber, lignin, cellulose, ash, calcium, phosphorus, and beta carotene. The information provided by these determinations should be of great practical value in most range forage evaluations. More information on certain minerals may be needed in areas where deficiencies are known to occur. Information concerning crude fat may be valuable for some shrub ranges containing plants with high true fat content.

An additional step in evaluating forage value is the determination of animal response. Palatability is also important, because it directly influences feed intake. However, some plants may be very valuable on the range even when their palatability is rather low if they contribute essential constituents, such as vitamins and minerals to the diet when other more palatable plants are deficient, in these nutrients.

Forage quality can be better evaluated by determining forage digestibility by various classes of ruminants. As previously described, there are many techniques for determining for-

age digestibility. The method of determining total digestible nutrients (TDN) should be replaced by energy determinations, because TDN does not adequately express the relative nutritive effect of roughages compared with concentrates (roughages are overevaluated). For direct or *in vivo* feeding trials, determinations of digestible protein and either digestible energy or metabolizable energy are recommended. Digestible energy is recommended over metabolizable energy if the forage does not contain appreciable amounts of essential oils because the technique is less complex; however, results are highly correlated to animal performance. Furthermore, in determining metabolizable energy, losses in methane gas must usually be computed rather than determined directly, which can further increase experimental error (Swift 1957).

Indirect methods can be used to calculate forage digestibility, which is often a decided advantage because, (1) much time and expense can be saved and (2) grazing animals can be studied under range conditions. Indicators are used in both the ratio and fecal index techniques, but there is some doubt about the effectiveness of indicators in determining digestibility coefficients. The use of chromogens as internal markers was unsatisfactory on some range plants evaluated by Cook and Harris (1951). Harris et al. (1959) found that the use of the lignin-ratio technique combined with chromic oxide capsules gave promising results during range forage intake and digestibility studies on sheep. Smith et al. (1956) had difficulty in determining lignin percentages of woody materials accurately and stated that there is no basis for using the lignin-ratio approach in studying winter diets of mule deer.

The use of artificial rumens—the *in vitro* technique—is a promising method for indirectly determining plant digestibility. Forage dry matter digestibility obtained by incubation with fresh rumen liquor usually compares well with *in vivo* digestibility. Protein can also be digested in the laboratory by the enzyme, pepsin (Miller 1961). Despite the advantages of the indirect methods, the most valid information is gained by relating results obtained from *in vitro* trials to those obtained from *in vivo* trials.

Rumen assays as described by Short (1966) are gaining popularity. The determination of volatile fatty acids (VFA) is a newer technique which greatly assists in evaluating quality of forages. A knowledge of digestion end products, particularly the proportion of the volatile fatty acids, produced from feed in the rumen will permit a more accurate estimation of animal response such as milk yield, fat gain, etc. (Shaw 1959).

Mott (1959), in discussing the factors involved in a grazing trial, said "output per animal is a function of nutritive value and rate of intake; nutritive value is a function of chemical composition and digestibility; and rate of intake is a function of palatability, chemical composition, digestibility, grazing pressure, and animal response to the environment."

Because a feed has a high nutritive content and is highly digestible does not necessarily mean that it satisfies the physiological demands of the animals ingesting it (Dietz 1965). Nutritional requirement and animal response studies are needed to obtain this type of information.

In summary, the quality of forage for range animals is determined by: (1) The palatability of the forage and related intake by the animal; (2) the levels of important nutrients in the portion of the plant eaten; (3) the ability of animals to digest these nutrients; and (4) the efficiency of the digested nutrients to meet the physiological demands of the animal for maintenance, growth, reproduction, fattening, and other processes and activities. In assessing forage quality for ranges primarily used by ruminant animals, the end results are measured by animal performance. This performance will be determined largely by the ability of the rumen micro-organisms to utilize efficiently the nutrients in the ingested feed.

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Nutrient Requirements of Livestock and Game

Lowell K. Halls[1]

This paper reports data mainly for beef cattle, sheep, and deer—the largest consumers of food from forests and rangelands of the United States. When available, information is included for other mammals and birds such as elk, antelope, goats, rabbits, squirrels, wild turkeys, and quail.

Maynard and Loosli (1956) cautioned against the use of the term "requirement" because it implies an exactness which does not exist. Strictly speaking, a requirement is the minimum amount of a nutrient that will promote a given body function to the optimum in a perfectly balanced ration. This minimum varies among animals and environments. An amount that is adequate in closely controlled experiments may not be sufficient in an environment that is not controlled. Despite limitations, nutrient-requirement standards are useful in selecting forage species, in formulating feeds, in evaluating the carrying capacity of ranges and pastures, and in determining the adequacy of a particular ration.

Much of the information on nutrition of domestic livestock is taken from the reports of the Committee on Animal Nutrition of the National Academy of Science–National Research Council (NAS-NRC). Unfortunately, similar appraisals are not available for game.

DRY WEIGHT OF FEED

The dry weight of food consumed by an animal normally is closely related to body size. For range livestock and big game, daily consumption is roughly 2 to 4 percent of live weight. Small mammals and birds eat up to 10 percent of their weight. In table 1, feed intake of several species is related to condition and body weight.

Consumption is influenced by many factors other than body weight. Grazing sheep require an average of 80 to 90 percent more feed for maintenance than sheep fed indoors (Joyce 1968). Older animals eat less per unit of body weight than younger animals (NAS-NRC 1963). Consumption also varies with food quality. Diets low in protein cause lowered food consumption (Madsen 1939). In south Georgia the daily intake of dry forage was 20 pounds per cow when forage was of relatively high quality but only 12 pounds per cow when quality was low (Hale et al. 1962). Even when quality is constant, food intake of some animals may vary seasonally (Fowler et al. 1968; Long et al. 1965). Feed intake may also differ among animals grazing apparently comparable forages. McCullough and Sell (1952) reported a daily intake of 16 pounds of dry matter by cattle on fescue pasture as compared to 26 pounds on a mixed-species pasture of similar quality. In extremely cold weather, wild animals may consume very little food (Silver and Colovos 1957). The amount of acetic acid in the rumen, the content of undigested feed residues in the digestive tract, and thermostatic mechanisms influenced food intake of ruminants (Conrad 1966).

To be most meaningful, information on intake should include species, size, age, and condition of animal; quality of food; and season of use. Data are not available for many wildlife species under the various conditions in which they live. Where information is extrapolated from one species and from one condition to another, care should be taken to compare only animals with similar metabolism and similar digestion capacity. For example, under like conditions, the food intake of goats, deer, and antelope may be similar. Domestic and wild turkeys probably have similar requirements, as do domestic and wild sheep and white rats and squirrels.

ENERGY[2]

Since all organic nutrients contain energy, it provides a common expression of the nutritive value of foods (Maynard and Loosli 1956).

Lack of digestible energy (DE) was the most common deficiency in the diets of sheep and cattle (NAS-NRC 1963, 1964). With the possible exception of a lack of protein and a lack of phosphorus, it is probably the most common nutritional deficiency of deer (Dietz important to other kinds of range livestock and wildlife. Low-energy intake causes reduced or halted growth, loss of weight, failure to conceive, increased mortality, and lowered resistance to parasites and disease.

Digestible-energy measurements do not consider energy losses from urine, combustible gases, and heat increment during digestion. As these losses are larger for roughages than for concentrates, a pound of DE in roughage has considerably less value than a pound in concentrates. On shrub ranges the use of DE

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[2] This section is abstracted in part from Short and Golley (1968).

TABLE 1.—*Animal requirements for daily feed, digestible energy, and protein*

Species and condition class	Reference	Body weight	Daily feed per Animal	Daily feed per Live weight	Digestible energy for maintenance	Protein
		Kg.	*Kg.*	*Percent*	*Kcal.*	*Percent*
			Beef cattle			
Steers and heifers, normal growth	NAS-NRC 1963	273	7.4	2.7	9,000	9.3
Mature pregnant cows, wintering	do	454	8.2	1.8	18,000	7.5
Cows nursing calves, first 3 to 4 months postpartum.	do	454	12.7	2.8	33,600	8.3
			Sheep			
Ewes, last 6 weeks of gestation	NAS-NRC 1964	55	1.9	3.5	4,400	8.2
Ewes, first 8 to 10 weeks of lactation.	do	55	2.3	4.2	5,800	8.4
Ewes, replacement lambs and yearlings.	do	55	1.5	3.4	3,400	7.6
			Deer			
White-tailed						
Body growth maintenance.	French et al. 1955	45	1.4–1.8	3–4	6,300 [1]	13–16 6–7
Mixed herd of white-tailed and mule.	Nichol 1938	45	1.1	2.4		
White-tailed	Dahlberg and Guettinger 1956.	45	1.6–2.5	3.6–5.5		
Do	Doult et al. 1966	45	.9–3.2	2.7		
Mixed herd, winter maintenance	Davenport 1939	45	.8–3.4	1.8–7.6		
White-tailed, maintenance and weight recovery, 3 1/2-year-old male:	Magruder et al. 1957	68–91	1.8		7,320 [1]	
Optimal growth, 2-year-old	do		2.0			
Optimal growth, yearling	do		2.5			
Black-tailed	Bissell et al. 1955	45	2.0	4.4	4,500	
			Wild Turkey			
Gobbler	Korschgen 1967	9.1	.3	3.3		
Growing	NAS-NRC 1966					20
Breeding	do					15
			Bobwhite Quail			
Breeding	Nestler 1949a					23
Growing	do					28
Nonproductive mature birds in winter.	do					12
Growing	Nestler 1949b	.14	.008	5.7		
Winter maintenance	Nestler 1949c	.16	.015	9.4		
			Squirrels			
Gray, pregnant	Uhlig 1955	.53	.07	13.2		
Gray, lactating	do		.07			
Gray, mature male	Short (study in progress).	.53	.03	5.7		
Fox	Baumgras 1944		.03			
Fox, mature male	Short (study in progress).	.87	.04	4.6		
Fox	NAS-NRC 1962	.35			115	15–20 [2]

[1] Gross energy requirements.
[2] Extrapolated from growth requirements of rats.

has been criticized (Harris et al. 1959) because the high essential oil content in some plants yields erroneously high DE values.

Especially in winter, energy requirements are somewhat higher for range animals than for animals on farm lots, because range animals must not only travel farther in search of food but must also maintain body temperatures without the aid of shelters (Stoddart and Smith 1955). Blaxter (1962) stated that a 500-kg. steer with a basal metabolism of 8,000 kcal. per day expends 50 kcal. more energy per

hour standing than lying, and that each time he stands and reclines he expends 12 more kcal. Young animals at play may require energy at a rate 10 percent above the fasting level, i.e., the basal metabolism requirements. Short and Golley (1968) reported that cattle may require 15 percent more energy for normal range activities than for fasting conditions, and that the energy demands of wild herbivores under usual range and climatic conditions may be at similar percentages above the fasting level.

The NAS-NRC (1964) reported that the energy required for maintenance is 24 to 77 percent higher for grazing sheep than for stall-fed sheep. Grazing sheep may require as much as 77 percent more energy than those maintained in pens or shelters (Grimes 1966). A foraging sheep that walks 6,400 m. and ascends 100 m. in a day's activity may need energy at a rate 20 percent above the basal level (Blaxter 1962).

Energy requirements are calculated from established metabolic constants. The basal metabolism of animals varying in size from mouse to elephant is proportional to body weight (BW) raised to the $\frac{3}{4}$ power (Byerly 1967). There is relatively little information on the energy metabolism of domestic ruminants at different levels of productivity (Flatt 1966; Flatt and Coppock 1965). Few, if any, energy metabolism studies have been undertaken with range livestock and wild herbivores; their energy requirements are often extrapolated from standards developed in livestock feeding trials.

In general, maintenance requirements of ruminants can be estimated as 1.36 kcal. of metabolizable energy per kcal. of fasting metabolism, or as about 1.7 kcal. of apparently digested energy per kcal. of fasting energy metabolism (Blaxter 1962). Using the interspecies mean of 70 kcal./BW (kg.)$^{3/4}$/24 hours and Blaxter's conversion factors, the estimated maintenance requirements for ruminants are 95.2 kcal. ME/BW (kg.)$^{3/4}$/24 hours or 119.0 kcal. DE/BW (kg.)$^{3/4}$/24 hours. Some caution should be exercised in using these standards, because it has been pointed out that maintenance requirements of sheep (NAS-NRC 1964), for example, are lower than those for other kinds of livestock (Byerly 1967). Digestible energy requirements for various animals are given in table 1.

Severe physical activity expends much energy, and sometimes more energy is spent in the search for food than can be gained from its digestion. Both body heat loss and coat insulation varies throughout the year. Wind, hair wetness, air temperature, and humidity modify heat loss and influence the metabolic activity required for necessary body warmth (Blaxter 1962). In very cold weather, conservation of heat may offer the best chance for survival of deer (Silver and Colovos 1957). Emaciated animals are sensitive to cold, but when they have access to roughage—even straw or dry, weathered range grass—the heat increment attained by its digestion will keep them warm and alive at −40°C. Without a source of feed energy, animals may die of cold at −23° C. (Byerly 1967). At −20° C. a 50-kg. deer can withstand more than twice as much wind velocity when on a full diet as when on a maintenance diet (Moen 1968).

The time and conditions under which feed is deficient in energy are greatly significant. In white-tailed deer, prenatal malnutrition retarded length and weight growth of the fetus. At birth the average weight of the fawns was 46 percent less and they tended to be stunted skeletally when compared to fawns from well-fed does (Verme 1963). In another study (Verme 1967), white-tails that were inadequately nourished in summer or autumn reproduced only one-third as rapidly as deer receiving good rations. Yearling white-tailed deer on limited amounts of feed for 10 weeks never attained the average body weight of deer on unrestricted feed or of deer on restricted feed for only 5 weeks (Long et al. 1959).

Short periods of feed deficiencies are not necessarily harmful. For example, calves from 3 to 8 months old can maintain their weight on rations that meet their nutritional needs, without later loss in efficiency of feed utilization or quality of meat (Winchester and Ellis 1957). In a study by Winchester and Howe (1955), a reduced feed intake by steers for 180 days did not change the amount of energy later required to reach a weight of steers fed *ad libitum*. Apparently the long-established practice of maintaining cattle and sheep through winters or droughts at low planes of nutrition is not harmful.

EFFICIENCY OF FOOD UTILIZATION

Fattening, growth, pregnancy, and lactation affect food and energy consumption and the efficiency of energy utilization above the maintenance level. The efficiency with which ingested materials are converted into fat is lowest for feeds with a high roughage content (Blaxter 1962). During lactation, the way in which food energy is utilized changes. Body fat is frequently converted to milk production by high-producing dairy cattle fed unlimited amounts early in lactation (Flatt 1966). At later stages of lactation, less of the ingested gross energy is utilized for milk production, and more is used to restore the depleted body reserves. Young animals are more efficient than adults in using food energy for growth.

Cows, sheep, and large wild ruminants may have similar abilities to digest common rations even though their food selectivity may differ. White-tailed deer and mule deer of North America (Short 1963), roe deer of Eurasia (Brüggemann et al. 1965), and several of the African antelope species probably digest fibrous foods poorly and may suffer when only fibrous forages exist on a range. Hungate (1966) mentions some differences in rumen fermentation rates among herbivores; these differences could affect forage digestion and range utilization. For mule deer, the available energy in a feed is inversely related to its cellulose content (Short 1966).

Horselike animals digest somewhat less food than ruminants. The difference is due largely to lower efficiency in digesting fiber, nitrogen-free extract, and fat components (Morrison 1950). Swinelike animals (except perhaps the hippopotamus) digest fiber even less efficiently than do horses.

Large rodents and lagomorphs are less efficient than ruminants in the digestion of fiber, and commercial rations for them frequently contain only 9 to 18 percent fiber (NAS-NRC 1962).

PROTEIN

Protein is essential for growth, weight gain, appetite, milk secretion, and regular oestrus. A liberal continuous supply is needed throughout life. When protein intake exceeds body needs of adult animals, nitrogen tends to be wasted since it can only be stored in very limited amounts. Therefore, protein is an expensive source of energy. During rapid growth, the body can utilize much more protein than the minimum requirement. The daily requirement increases with age and size, at least during early growth, but it decreases per unit of weight and in relation to the energy requirement (Maynard and Loosli 1956).

Protein requirements included in most livestock feeding standards were determined from feeding trials (table 1). They generally show that 0.27 kg. of digestible protein per 45 kg. of BW is sufficient for cattle and sheep.

In NAS–NRC standards, a digestion coefficient of 55 percent is used to calculate digestible protein from total protein. Perhaps the conversion factor should be less for range cattle and sheep because of the low protein digestibility of poor-quality range forages.

Protein requirements of wild animals are probably at least equal to those of domestic species. If crude protein levels in deer forage fall below 6 to 7 percent, rumen functions are seriously impaired (Dietz 1965). In Missouri deer fed diets containing 7-percent protein developed slower and had poorer breeding condition and fawn survival than deer fed more protein (Murphy and Coates 1966). In Michigan a diet containing 12.7 percent crude protein did not permit maximum weight gains in male fawns, but it was adequate for female fawns (Ullrey et al. 1967).

Dietary protein levels for white-tailed deer have been suggested as 13 to 16 percent for optimum growth and as 6 to 7 percent for maintenance (French et al. 1955). On southern ranges during most of the year, the protein content of browse is below the level suggested for deer growth (Blair and Halls 1968; Halls et al. 1957). Requirements for game birds are higher than for deer, ranging up to 28 percent for growing bobwhite quail (Nestler 1949a). For omnivorous species such as wild pigs, and most rodents, a diet which encourages healthy growth must have a protein content of approximately 15 percent (Wackernagel 1966). According to NAS–NRC (1962), large rodents and lagomorphs require protein levels of 15 to 20 percent for growth and reproduction.

WATER, MINERALS, AND VITAMINS

Water

Water is necessary in transportation of metabolic products, in secretion and excretion, in regulation of body temperature, and in many other body processes.

Requirements for animals may be satisfied through free water, dew, water in feed (succulence), and metabolic water. Consumption by animals varies widely and depends on such factors as temperature, rainfall, activity, age, stage of production, respiratory rate, frequency of watering, consumption of feed, plane of nutrition, and composition of feed. The immediate effect of water restriction is to lessen food consumption and thus reduce growth and food efficiency (Crampton and Lloyd 1954). It is best to give domestic animals free access to all the water they desire.

Wild species vary widely in their water requirements (Leopold 1947). Eastern white-tailed deer require drinking water occasionally; nursing females need it daily. Western races of white-tails apparently can subsist on succulence alone. Mule deer can subsist and fawn on succulence alone. Does search for water during fawning, and all mule deer seek it after frost reduces succulence. Elk and antelope have water needs similar to those of mule deer; they drink regularly when possible, but they can subsist and reproduce on succulence alone. These animals may need drinking water during droughts, when succulence is reduced.

Birds need less water than mammals and are

usually less sensitive to shortages. The requirements presented here for game birds were taken mainly from Edminster (1954). Sage grouse drink water when it is available, but they can live for many days without free water and even without dew. However, good populations occur only in habitats that have a supply of free water. The sharp-tailed grouse's needs are met by succulence and dew. These are also adequate for prairie chicken, except during extreme droughts.

Bobwhite quail exist with succulence and dew in humid areas, but the western limit of their range may be determined by a lack of water. Water is usually no problem for the bobwhite within its main range, but many birds may die during droughts. Other than in the humid coastal belt, California quail require free water during the hot, dry summer. They must be within 300 yards of water during nesting and brooding. Gambel's quail subsist on succulence and dew, but on ranges that lack succulent plants they must have free water at approximately 4-mile intervals. Mountain quail need water close by in the summer brood period, and chicks must have water daily. Scaled quail are probably more exacting in water requirements because they feed less than other quail on succulent plants. They are rarely found more than 1 mile from free water during dry periods.

Hungarian partridge subsist on dew. Chukar partridge require water in the summer and at other times when succulent vegetation is lacking.

The eastern turkey requires drinking water, but the southwestern turkey can apparently subsist on dew and succulence.

Doves need free water.

Minerals

Salt.—Sodium and chlorine help maintain water metabolism, osmotic pressure, acid-base equilibrium, and passage of nutrients into cells. Only a little information is available on the exact salt requirements of animals. Farm animals are usually given all the salt they want. Intake is usually from 0.2 to 0.6 weight-percent of their ration (table 2). Excessive salt intake can kill, but as much as 2 pounds can be consumed daily by cows without deleterious effects, provided there is an abundant supply of good water (NAS-NRC 1963).

Animals deprived of salt develop a craving and may resort to chewing wood, licking soil, and similar manifestations. Some range managers believe that animals may eat normally unpalatable, poisonous plants when deprived of salt. Prolonged salt deficiencies cause lack of appetite, unthrifty appearance, decreased feed consumption, and inefficient feed utilization.

Big game animals can exist without supplemental salt, but they frequently use natural and artificial salt licks.

Some birds require salt (Edminster 1954). Nestler (1949b) reports that a diet containing 0.25 to 1 percent salt produced better quail weights than a salt-free diet. The amount needed can best be extrapolated from nutrient requirements of poultry (NAS-NRC 1966).

Calcium and phosphorus.—The principal function of these minerals is the formation of a skelton. Adequate calcium and phosphorus nutrition depends upon a sufficient supply of each element, a suitable ratio between them, and the presence of vitamin D. A desirable ratio is between 1:2 and 2:1. Adequate vitamin D decreases the importance of the ratio and increases the efficiency of utilization. Domestic herbivores need more calcium than phosphorus for early growth, but the ratio of the two requirements decreases as maturity is approached (Maynard and Loosli 1956). Wild herbivores that annually produce antlers need both abundant calcium and phosphorus for this development.

A depraved appetite with a specific craving for bones is evidence of a prolonged phosphorus deficiency in an animal. Symptoms of calcium deficiency are usually inconspicuous.

Phosphorus deficiency in forage is widespread through the United States but, except in the Southeast, calcium deficiency is comparatively rare. Young, growing animals have a much higher requirement than adults. To a certain extent, animals can store these elements. Maynard and Loosli (1956) state that, per pound of air-dry feed, calcium requirements range from 0.15 to 1 percent, and phosphorus from 0.15 to 0.6 percent. The latest NAS-NRC standards indicate that the requirements for these elements may be higher in some mammals and birds and in particular stages of growth and reproduction (table 2).

The needs of rumen micro-organisms in promoting high rates of live-weight gain in cattle suggest minimums of 0.20 percent phosphorus in finishing rations and 0.15 percent in other rations (NAS-NRC 1963).

Calcium and phosphorus requirements for big game appear to equal or exceed those for livestock. White-tailed deer survived on rations containing 0.25-percent phosphorus and 0.30-percent calcium. Best antler growth, however, was obtained when rations contained 0.56-percent phosphorus and 0.64-percent calcium (Magruder et al. 1957). Calcium and phosphorous requirements for other antler-producing big game probably are similar to those of white-tailed deer.

Deer browse in southern forests contains much less than 0.25-percent phosphorus

TABLE 2.—*Water, mineral, and vitamin requirements of selected animals and birds*

Condition class	Reference	Body weight	Water	Minerals			Vitamins	
				Ca	P	Salt	A	D
		Kg.	*Liters*	(*Percent of ration*)			(*IU/kg.*)	(*IU/kg.*)
			Beef Cattle					
Steers and heifers, normal growth.	NAS–NRC 1963	273		.21	.16	.25	1,650	
Mature pregnant cows, wintering.	do	454		.16	.15	.50	2,200	
Cows nursing calves, first 3 to 4 months postpartum.	do	454		.24	.18	.50	3,300	
Range cattle	Stoddart and Smith 1955.		28–38					
			Sheep					
Ewes, last 6 weeks of gestation.	NAS–NRC 1964	55		.23	.17	.6	1,426	156
Ewes, first 8 to 10 weeks of lactation.	do	55		.28	.21	.5	1,197	132
Ewes, replacement lambs and yearlings.	do	55		.20	.18	.6	814	163
Range sheep	Stoddart and Smith 1955.		0.95–5.7					
			Deer					
White-tailed, 2-1/2 to 3-1/2-year-old bucks.								
Survival	Magruder et al. 1957.			.30	.25			
Best antler development.	do			.64	.56			
Black-tailed	Bissell et al. 1955	45	2.3					
			Turkey					
Breeding	NAS–NRC 1966			2.25	.75		4,000	900
Starting poults	do			1.20	.80	.40	4,000	900
Growth	do			1.20	.80	.40	4,000	900
			Bobwhite Quail					
Starting and growing	NAS–NRC 1966					.40	13,000	
Breeding	do			2.3	1.0			
			Squirrel [1]					
Growth	NAS–NRC 1962			.6	.5	.25	2,000	
Gestation and lactation	do			.6	.5		12,000	

[1] Extrapolated from requirements of rats.

(Blair and Halls 1968; Halls et al. 1957). Thus, it appears that deer can exist on ranges where a major source of their food is below the recommended level for maintenance.

Game birds, and perhaps squirrels, need considerably larger proportions of these elements than do large mammals (table 2).

Minor elements.—Several minor elements are essential to animal growth and reproduction, but the amounts needed are not well defined for many animals. Unless indicated otherwise, the several requirements for minor elements are taken from Maynard and Loosli (1956) or NAS-NRC (1962, 1963, 1964, 1966).

Magnesium is an essential constituent of bones and teeth and is an activator of various enzymes. Chicks and beef calves need about 0.05 percent in their diets, and dairy calves require about 0.6 g. per day per 45 kg. of body weight. Rations or forages containing 0.06 percent, or about 1.52 g. per day, are considered adequate for sheep. Deficiencies are rare except where there are severe imbalances between magnesium and calcium and magnesium and phosphorus. "Grass tetany" and "grass staggers" are sometimes attributed to magnesium deficiencies.

Sulphur is required by the animal body in the form of sulphur-containing amino acids. Sulphur requirements for mature ewes are about 0.08 to 0.1 percent of their total ration. Since most feedstuffs contain more than 0.1-

percent sulphur, it is not likely to be deficient for most animals.

Potassium functions in the same general way as sodium and chlorine. Rats, pigs, and chickens need potassium levels of approximately 0.2 to 0.3 weight-percent of the dry ration.

Iodine is necessary for proper functioning of the thyroid gland. Levels high enough to prevent goiter range between 0.002 to 0.004 mg. per kg. of body weight. Growing quail and pheasants need about 0.30 mg. per kg. of feed.

As a constituent of hemoglobin, iron is essential for the functioning of every organ and tissue in the body. Rations containing 100 to 200 mg. of iron per kg. of feed are ample for sheep and cattle. Chickens require about 18 mg. per kg.; however, young turkey poults require about 60 mg. per kg. of feed. Iron deficiency often causes anemia.

Copper is neccessary for hemoglobin formation. Deficiency symptoms vary by species. Requirements are approximately 1.8 mg. per kg. of feed for poultry, 4 to 8 mg. per kg. of feed for cattle, 5 mg. per day for sheep, and 2 mg. per day for pigs.

Cobalt is important in the synthesis of vitamin B_{12}, which combats anemia and improves growth. Animals appear to need about 0.2 mg. per kg. of body weight daily. Deficiency symptoms include anemia, loss of appetite, weakness, emaciation, and eventually death.

Manganese is essential in reproduction and in bone formation. Beef cattle appear to require about 5.4 to 9.0 mg. per kg. in air-dry ration, and breeding turkeys need about 33 mg. per kg. of feed.

All animals require some zinc. The exact amount for most species is unknown, but zinc is rarely deficient in diets. A diet containing 100 p.p.m. of zinc alleviated the clinical symptoms of deficiency in sheep.

In the absence of specific information on the minor-element requirements of game, it must be assumed that big game need about the same quantities as cattle and sheep, and that game birds need about as much as domestic poultry.

Vitamins

Vitamin A.—Plants do not produce vitamin A, but they contain its precursor, carotene, which is converted into the vitamin in animals. Much of the carotene is lost during curing of roughage, and it is often deficient in late-winter food. Vitamin A can be stored in the liver and also as carotene in body fat. Animals on nutritious green forage store extensive reserves for the winter, when the diet may be deficient. The rate of vitamin A storage on a high-intake diet can greatly exceed the rate of depletion on a vitamin-deficient diet. Lambs pastured on green feed, for example, store up to a 200-day supply of vitamin A in their livers.

Vitamin A requirements listed in table 2 for sheep and cattle probably are about the same as those of big game. Game birds need relatively high levels of vitamin A (table 2), and high mortality of quail occurred in Texas when food was deficient in this nutrient (Lehmann 1952).

Vitamin D.—Vitamin D is formed by the action of radiant energy on ergosterol and cholesterol in amimals.

The amount of vitamin D needed varies with the relative mineral concentrations in the diet and with the species. Requirements for beef cattle are estimated to be about 300 IU per 45 kg. of live weight, and for sheep about 250 IU per 45 kg. of live weight.

Turkeys and pheasants need more vitamin D than chickens.

Vitamin D promotes retention of calcium and phosphorus in blood and tissue. The body can store some of this vitamin.

Vitamin D is unlikely to be deficient in animals in the open during the summer. The most critical time is winter, when days are short and cloudy, and when the sun's rays are least concentrated.

CONCLUSIONS

Animal "nutrient requirements" are useful standards for selecting forage species for evaluating the carrying capacity of ranges, and for determining the adequacy of rations for animal maintenance, growth, reproduction, and fattening. The requirements are not exact because they are influenced by many ever-changing factors, such as size, activity, age, and condition of the animal; quality of food; season of use; and weather.

Digestible energy is the most common deficiency in the diet of range herbivores. Reasonably good energy standards have been developed for livestock under controlled conditions, but similar information is generally unavailable for wild ruminants. In the future the emphasis in nutrition research should be to establish energy requirements under range conditions.

Even though much research has gone into finding the animal requirements for protein, calcium and phosphorus, the standards for range animals, particularly wild ruminants, are not well established. In some cases the minimum requirements seem inconsistent with the quality of forage ingested on ranges supporting healthy animals.

Game birds and small mammals generally have higher requirements than large ruminants for protein, phosphorus, and calcium,

but their water needs are less exacting. Nutritional information about these groups of wildlife are often extrapolated from domestic fowl and laboratory animals; thus, needs under range conditions are not well known.

Native forage usually contains sufficient minor elements to satisfy the needs of range animals; however, certain elements may be locally deficient.

Vitamins A and D may be deficient in late winter on ranges where green feed is sparse and when the weather is cloudy.

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Manipulation of Forage Quality: Objectives, Procedures, and Economic Considerations

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Most rangeland-management practices influence quality of forage. This paper describes measures applied specifically to alter nutrient content, palatability, season of growth, or digestibility. The objective of such manipulations is usually increased consumption of nutrients by livestock, improved distribution of grazing, or both. However, on sites sensitive to grazing, palatability of forage is sometimes intentionally depressed to minimize damage.

METHODS OF REGULATING QUALITY

Fertilization

Few, if any, methods for improving forage quality have recently received more attention from range investigators than fertilization. Studies of herbage responses to nitrogenous and phosphatic fertilizers have predominated; efforts have been directed mainly toward remedying deficiencies of protein and phosphorus.

In many trials the application of nitrogen, either alone or with phosphorus, has materially increased protein content of forage. On a pine-bluestem range in the humid South, nitrogen increased protein in mature herbage by one-third (Duvall and Grelen 1967). Favorable responses have also been reported for climatic zones ranging from subhumid to arid (Cosper *et al.* 1967; Freeman and Humphrey 1956; Powell and Box 1967).

Even heavy applications of nitrogen are often quickly expended or lost by leaching, and the quality of subsequent growth declines sharply. Periodic fertilization with small quantities usually benefits quality more throughout the growing season than a single heavy application, but the cost of spreading becomes prohibitive. Hydrocarbon carriers that slowly release fertilizer elements have recently shown promise on turf grasses (Skogley and King 1968) and may prove useful on forage species.

In humid regions, increases in herbage phosphorus following application of phosphate have been even more spectacular than protein gains after adding nitrogen. On Florida range, rock phosphate increased phosphorus content of several important grasses about sixfold (Lewis 1963). As with nitrogen fertilization, forage response to phosphorus application has not been confined to areas of high rainfall. Superphosphate on desert grassland in Arizona materially increased phosphorus in the predominant grasses (Freeman and Humphrey 1956).

Much of the fertilization research has been primarily concerned with forage response during the growing season, whereas protein is most often deficient in winter forage. In certain instances the deficit may be remedied by fertilization. In a Texas trial (Dee and Box 1967) most grasses that received ammonium nitrate in June contained adequate protein for pregnant cows throughout the following winter; without fertilization protein was deficient from December until new growth appeared.

Fertilization has also lengthened the green-feed period. Lavin (1967) found that application of ammonium nitrate on seeded range in the southwestern ponderosa pine zone extended the growing season into late summer and fall. Freeman and Humphrey (1956) reported somewhat similar results for desert grassland.

Some responses to fertilizer may be greater on forested range than on grassland. Burton *et al.* (1959) reported that increases in protein and calcium and a reduction in available carbohydrates accompanied both fertilization with nitrogen and reduction of light intensity. These changes were greatest when a low intensity of light was combined with a heavy application of nitrogen.

Fertilization may improve digestibility of critical nutrients in forage. For instance, on a pasture in south-central Washington, protein digestibility for cattle was higher in herbage receiving 100 pounds of nitrogen per acre than in herbage growing without nitrogen fertilizer (Heineman and Evans 1966). Matrone *et al.* (1949) reported that protein digestibility for sheep was greater in fertilized than in unfertilized forage, with the difference entirely attributable to the gain in protein content of the fertilized forage. Mitchell (1942) also reported a positive correlation between apparent digestibility of protein and the quantity present. Thus, where fertilization improves protein content, digestibility of that nutrient may also increase.

Grazing distribution can be altered by fertilizing. Utilization of desert grassland was about three, four, and five times greater with 25, 50,

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and 100 pounds of nitrogen per acre than without fertilizer (Holt and Wilson 1961). Applying 67.5 pounds per acre of nitrogen on mountain range increased use from 15 to 73 percent during the season following treatment, and the carryover effect was significant during the second year (Smith and Lang 1958).

Herbage Removal

It has been well established that the quality of forage diminishes as the plants mature. Methods for minimizing old and for maximizing new herbage include burning and intensifying grazing pressure.

Fire is widely used, particularly in regions of moderate to heavy rainfall. Burning a pine-bluestem range in Mississippi during the winter increased the content of crude protein, ether extract, calcium, and phosphorus in new herbage (Wahlenberg *et al.* 1939). On bluestem prairie in Kansas, burning in midspring increased both the crude protein and ash and decreased the ether extract (Smith and Young 1959).

Effects of burning may vary considerably with season of treatment. In a comparison of late-winter, spring, and midsummer fires on pine-bluestem range, the protein content of herbage produced during the 30 days after fire was greatest for the summer burn and least for the winter burn (Grelen and Epps 1967). Also, in midwinter protein content was almost 1.6 times greater for range burned the previous summer than for that burned the previous winter. These findings suggest that burning different parts of a range unit at intervals from late winter until midsummer could provide forage of relatively high quality throughout most of the growing season. Also, burning in midsummer and deferring use until winter could materially reduce requirements for protein supplement.

Burning destroys old herbage, thereby improving accessibility of new growth. With the insulating effect of litter reduced, the average soil temperature is higher during spring on burned than on unburned grassland. Hence, growth begins earlier on burned areas (Kucera and Ehrenreich 1962).

Cattle usually prefer herbage on recent burns to that on unburned areas. On pine-bluestem range burned in 3-year rotations, 78 percent of the herbage grown in the season following fire was utilized (Duvall and Whitaker 1964). In the second and third years after fire, use averaged only 31 and 18 percent. Similar findings have been reported for pine-wiregrass range (Shepherd *et al.* 1953) and tall-grass prairie (Aldous 1934). Thus, fire can help regulate grazing distribution.

Digestibility of certain nutrients in forage may increase following fire. Spring burning of bluestem range resulted in greater apparent digestibility of crude fiber, dry matter, and ether extract (Smith *et al.* 1960).

In trials with many range grasses, frequency of harvesting has been positively correlated with protein content of herbage (Newell and Keim 1947). Repeated clipping increased ether extract and phosphorus, as well as protein, in short-grass vegetation; it decreased nitrogen-free extract, but had little effect on calcium, ash, or crude fiber (Dickson *et al.* 1640).

These findings suggest that intense use during the growing season, like frequent clipping, limits accumulation of mature forage and may therefore improve quality. However, unless heavy grazing is alternated with periods of either deferment or rest, it is usually detrimental to vegetation. Since quality diminishes on unused range, intense grazing is most beneficial where high-quality forage is urgently needed during the growing season and where mature herbage satisfies requirements during other periods. In the South, where protein content of moderately grazed forage declines sharply after early summer, a system combining rotational burning and intensive use has been successful (Duvall and Whitaker 1964). Grazing trials in other regions are providing a growing list of cover types that tolerate intense use for brief periods (Laycock 1967; Springfield 1963).

Seeding

Seeding may benefit quality in various ways In Utah, the grazing season was more than 6 weeks longer on seeded grass than on native vegetation (Passey and Winn 1953). Incorporating seeded units into a management program for Colorado range prolonged the green-feed period and thereby increased weaning weights by an average of 32 pounds per calf (Currie 1966). Cattle grazing seeded western wheatgrass on southern Great Plains range required less than half as much supplemental protein as those on unseeded range (Pearse *et al.* 1948).

Grasses have been used almost exclusively in range seeding. Since the nutritive value of forbs frequently surpasses that of grasses, mixtures containing palatable forbs may improve quality more than grasses alone. For cattle grazing native Nebraska vegetation containing 31 percent forbs, these plants furnished 44 percent of the dry matter consumed but supplied greater proportions of the principal nutrients: calcium, 59 percent; phosphorus, 56 percent; soluble carbohydrates, 48 percent; and crude protein, 46 percent (Hoehne

et al. 1968). California range interseeded with subterranean clover produced forage with protein content equal to that of resident grasses fertilized with 80 pounds of nitrogen per acre; also, protein content remained high longer on the interseeded areas (Jones and Winans 1967).

Control of Overstory

Livestock on forest range usually graze openings and sparsely wooded areas much more intensely than well-stocked timber stands. For example, McEwen and Dietz (1965) found that only 8 percent of the herbage on forested sites was utilized, compared to 42 percent on nearby meadows.

Grazing may be intensified on underutilized, heavily wooded sites by sharply decreasing the overstory density. Such treatment may influence palatability and nutrient content of forage. Several investigators have shown that herbage in the open contained less protein and phosphorus than that under canopies (Cook and Harris 1950; McEwen and Dietz 1965; Vallentine and Young 1959), but the effects of overstory on other nutrients have been inconsistent. McEwen and Dietz reported that on Black Hills range in South Dakota, calcium and crude fiber contents were greatest for canopied sites, while the level of nitrogen-free extract was highest for open sites. In the Edwards Plateau of Texas, Vallentine and Young found that crude fiber content was greatest on open sites, whereas calcium and nitrogen-free extract values were similar for canopied and open sites. Differences in overstory composition —i.e., ponderosa pine in the Black Hills and oak-juniper in the Edwards Plateau—may have accounted for these apparent discrepancies.

Removal of overstory may increase digestibility of forage. In a Georgia experiment, on pasture with low-level nitrogen fertilization (Burton *et al.* 1959), lignin content of grass increased as intensity of light was reduced.

Curing of Forage

To avert the reduction in quality that accompanies maturation, forage may be harvested at the optimal stage of growth and stored for subsequent use. However, physical features that impair harvesting and low yields often make this procedure impractical.

Recently, interest has developed in chemical curing of range herbage. Bipyridylium herbicides have reportedly arrested maturation and thereby improved quality of the standing crop for use after the growing season. In Oregon trials (Sneva 1967), protein in range grass treated with 0.2 pound per acre of paraquat cation declined only 10 percent from June to October, whereas grass curing naturally during this period lost about half of its protein.

Application of Attractants and Repellents

Attractants have stimulated consumption of unpalatable forage. Spraying either molasses or a molasses-urea mixture on mature annual grasses resulted in complete utilization, while unsprayed foliage was grazed little (Wagnon and Goss 1961). Similar results have been reported for tobosagrass treated with molasses (Reynolds 1955).

Certain chemical coatings applied to foliage may inhibit utilization and thereby protect sensitive vegetation from grazing. In the South, several formulations containing chemicals normally used as fungicides reduced browsing of pine seedlings by cattle (Duncan and Whitaker 1959). Similar treatments could presumably reduce palatability of herbaceous vegetation.

Altering Species Composition of Native Vegetation

Reduced stocking, redistributed grazing, brush control, and specialized grazing systems have, according to various investigators, materially improved botanical composition. However, such practices usually have also increased yield, and this confounding has largely precluded evaluation of gains in quality.

COST-RETURN RELATIONSHIPS

With a few notable exceptions, e.g., chemical curing and application of repellents and attractants—treatments to improve quality also increase yield. Therefore, financial benefits, like biological responses, are difficult to determine. Even so, reasonably firm conclusions are possible regarding economic feasibility of certain practices.

Evidence favoring fertilization of native range has been far from overwhelming (Rogler and Lorenz 1957). Even with substantial improvement in both production and nutritive value, several investigators have either reported financial deficits or conceded that economic advisability was doubtful (Burzlaff *et al.* 1968; Duvall and Grelen 1967; Freeman and Humphrey 1956; Herbel 1963; Rogler and Lorenz 1957).

Most researchers who reported costs and returns of nitrogen fertilization found that gains in animal production were not sufficient to justify treatment. For northern Great Plains range, Rogler and Lorenz (1966) reported that the amount of protein differed most between fertilized and unfertilized forage early in the

growing season, when content was adequate without treatment. Later, when protein levels were lower, the increase attributable to fertilization was inadequate to appreciably affect gains by cattle. Undoubtedly, this problem is widespread.

Addition of phosphate, like that of nitrogenous fertilizer, seldom increases nutrient content enough to increase profits from livestock. In a study in southern Texas (Black *et al.* 1949), remedying the deficiency of phosphorus by fertilization gave greater returns per acre than feeding supplemental phosphorus to cattle. Whether this difference was attributable to increases in the phosphorus content of forage remains doubtful. However, a later study (Reynolds *et al.* 1953) revealed that the fertilized range yielded much more herbage than the unfertilized range.

In the South and Southeast where burning is common, Biswell (1958) reported that costs average $0.22 per acre. The expense of burning pine-bluestem range in Louisiana was about $0.15 per acre, with half chargeable to timber production (Halls and Duvall 1961). Since these costs are much less than for most treatments for improving forage, prospects for profit appear good. However, an increase in quality alone may prove insufficient to justify treatment. Steers grazing range in Mississippi that was burned annually averaged 46 percent greater gains than those grazing unburned areas. Yield of the principal grasses more than doubled with burning, and this increase undoubtedly accounted for much of the return (Wahlenberg *et al.* 1939).

Even the cost of prescribed fire may exceed the value of benefits accrued. A high proportion of burns on foothill range in California proved uneconomical. Costs averaged $3.65 per acre for 40-acre tracts (Sampson and Burcham 1954).

The cost of controlling nutritive value by manipulating grazing pressure varies greatly. On ranges where existing facilities suffice with little or no modification, returns from increased grazing values may exceed costs. Where extensive cross-fencing and water development are required, costs often are prohibitive.

Where grazing can be redistributed so that substantial quantities of forage that would otherwise remain ungrazed are used, prospects for economic gain are usually good. Whether manipulation of palatability is the best choice of methods depends largely on cost and effectiveness of alternatives—e.g., cross-fencing, herding, water development, relocation of salting and feeding stations, and development of trails.

Seeding grass to extend the green-feed period on Colorado range cost $8.50 per acre and increased returns by $7.70 per calf; with 90-percent calf crops and 6-percent interest, profits would repay the initial investment in 11 to 12 years (Currie 1966).

Returns from improvements in nutrient content through seeding have rarely been determined. Forage on sites selected for seeding trials has usually been seriously depleted. Therefore, an increase in forage production has been the main objective, and the combined effects of increased quantity and improved quality have been assessed.

Little is known about costs and returns for chemical curing of range forage. Moreover, herbicides of the type used for experimental treatments have not yet been cleared for consumption by livestock (Sneva 1967).

CONCLUSIONS

Although forage quality can be improved by various methods, the gains from the improvements have seldom exceeded the costs of treatments. Therefore, for the present, range managers should probably choose measures that will increase grazing capacity, and should relegate increased quality to a secondary objective. Much is already being done to raise the carrying capacity of ranges. When the possibilities for profitably increasing forage yields are exhausted, quality will assume added importance. Because research must be ahead of practice, techniques for improving quality should be developed now.

Technological advances are providing new opportunities for experimentation. For example, controlled-release fertilizers and chemicals that have potential for curing forage are being developed. Even-aged forest management that permits intensive control over forage variables on forest ranges has been widely adopted. Surface fungicides have protected plants from livestock for short periods, and new systemic fungicides may give enduring protection on sensitive sites.

Several old lines of research need expansion. Economic study has lagged far behind biological investigation. Relatively few techniques for controlling characteristics of fire have been applied to ranges. Too often, conclusions regarding response of vegetation and animals to burning have been based either on a wildfire or on a single prescribed fire. Only a few of the theoretically sound combinations of grazing intensities and seasons for their use have been investigated.

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Significance of Forage Quality as a Tool in Wildlife Managment

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INTRODUCTION

In the scriptural reference of Isaiah 40:6 ". . . all flesh is grass. . .," the author likened the destructibility of flesh to that of grass, although he may have also understood the physiological conversion of grass to flesh. The quotation, however, is an appropriate introduction to the presentation.

The fundamental relation of vegetation to animal life is effectively stated by Komarek (1966) of the Tall Timbers Research Station:

> All species of wildlife, in the final analysis, are dependent on vegetation in one way or another. Man, himself, in the final analysis, is dependent for his very existence, directly or indirectly, on plant life. If vegetation is basic, then man prospers in direct proportion to his skill in managing that vegetation. Again, if vegetation is basic, then wildlife prospers in direct proportion to man's skill in managing the vegetation. If this is a valid summation, then research concerning the manipulation of vegetation to determine wildlife response should be of major import to the wildlife management profession and to the whole field of wildlife conservation.
>
> Komarek goes on to describe the similarity of wildlife management, forestry, and agriculture as they relate to management of vegetation. He states, ". . . you cannot have a forest without trees, or you cannot have a farm without fields or pastures, but you can have a forest lacking wildlife. What is it that produces abundant wildlife on the farm and in the forest? Essentially, it is the composition, quality, and arrangement of the vegetation. Wildlife management, therefore, is a form of landscape management."

Of all factors affecting wildlife production, the supply and maintenance of quality forage is perhaps the most challenging to the wildlife manager. What, then, is the practical application of forage quality as a tool of wildlife management?

In habitat management, there are minimum levels of each element of nutrition, and there are optimum nutritional levels which play a key role. With an understanding of the cause-and-effect relations between forage quality and animal productivity, the land manager is in a position to translate knowledge into action. Various cultural improvement practices can be applied to enhance the quality of forage.

Wildlife habitat management techniques are usually positive from the standpoint of wildlife, but they may be negative from the standpoint of other resources. For example, the most important precaution on livestock ranges of the Southeast—to protect habitat for deer, turkey, and small game animals—excludes cattle from hardwood bottom lands (USDA/ 1968). This action is needed to protect the critical or quality wildlife foods from livestock.

Inadequate supplies of nutritional foods for big game animals often damage timber resources. For example, on the Tillamook burn in western Oregon, browsing damage to planted Douglas fir seedlings coincides with the period of snow cover (from about December through early March). During this period, trailing blackberry, the most preferred species, is largely unavailable under snowfall. Thus, the degree of tree regeneration damage incurred helps determine the level of deer harvest planned on high-value timber-producing lands. (Oregon State Game Commission 1968.)

EFFECT OF FORAGE QUALITY ON ANIMAL PRODUCTION

The inherent reproductive capacity of wildlife populations is seldom, if ever, achieved in nature. Decimating or inhibiting factors are at work throughout the prenatal and postnatal periods of life. Direct losses resulting from malnutrition are spectacular and self evident and can usually be measured with some degree of accuracy. However, less obvious losses, also have a direct effect on productivity as well as mortality in wildlife populations.

Cheatum and Severinghaus (1950) found that fertility of deer, based on embryo and ova counts, corresponded with the quality of the range being used. Measurements of fertility of white-tailed deer afforded an indicator of trends in population density in relation to range adequacy. These conclusions were later confirmed by Julander et al. (1961) in studies of mule deer on Utah ranges. Deer productivity on excellent summer range, compared with

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that on poor summer range, showed significant differences in fawn-doe ratios, percentage of multiple births, and productivity in the yearling age class. Productivity in this youngest producing age class reflects range condition more sensitively than does productivity of older age classes.

Hungerford (1964), in studies of Gambel's quail in southern Arizona, found that late winter and early spring moisture was closely correlated with breeding, rate of production, and survival of young birds. The early moisture induced production of green food, which, in turn, produced more vitamin A for storage in the liver.

As stated previously, mortality is the most spectacular manifestation of poor-quality forage. In the chaparral range of northern California, the principal period of mortality in deer is midwinter. Late summer and fall dieoffs occur after unusually hot summers. In either case the loss is associated with poor forage conditions and dietary deficiencies (Taber and Dasmann 1958). Swank (1958) found similar relationships of mortality to poor forage quality in deer studies in Arizona. Robinette et al. (1952), in studies on Utah ranges, found that winter deer losses varied inversely with forage quality. In the Jawbone deer herd study, Leopold et al. (1951) found that deer had such a strong attachment to a home range that they would not shift to higher quality forage even to survive.

Some forage species have a high nutritive content, but partly inhibit rumen micro-organisms (Dietz et al. 1962). Sagebrush, for example, is highly nutritious when fed in combination with other browse species. However, when it is fed alone, it produces harmful effects or malnutrition.

IMPROVEMENT OF FORAGE QUALITY THROUGH PRACTICES

Timber Cutting.—Clearings for wildlife in extensive timber types are an accepted improvement practice in the Eastern United States. This practice is widely used on National Forests and is used to a lesser extent on State and private lands. The principal objective in making such clearings is to remove patches of the overstory so that sunlight will reach the herbaceous vegetation to increase its abundance and nutritional value for wildlife. Clearings also result in better composition of low-growing plants and afford opportunities to grow planted forage crops of high nutritional value for both deer and small game species.

In hardwood forests, cuttings often produce vigorous stump sprouts palatable to deer. On the Pisgah National Forest, N.C., deer preferred sprouts over the more abundant seedlings (Moore and Johnson 1967).

If properly planned, clearings resulting from timber sales can serve the same purpose as clearings made specifically for wildlife. The principal difference is that timber sale cuttings form transitory openings, lasting 10 to 20 years, whereas clearings made specifically for wildlife are generally maintained as permanent openings. Clearings are expensive to establish and to maintain. This indicates the need to plan and to utilize cuttings in timber-sale areas for their multiple benefits.

On the Black Hills ranges in South Dakota, livestock showed a decided preference for forage grown on open meadows compared with that grown under ponderosa pine. Studies of chemical composition of plants grown on both sites disclosed generally higher levels of protein, crude fiber, calcium, and phosphorus in plants grown under timber. On the other hand, plants growing in the open had higher levels of nitrogen-free extract. The heavier grazing use in the meadows was attributed to the higher percentage of nitrogen-free extract (McEwen and Dietz 1965.)

Deer population estimates of the Forest Service indicate a 4-fold increase in black-tailed deer on the National Forests in Oregon since the mid-1940's, when patch-cutting of Douglas-fir timber got under way on a large scale. Even today, the preferred feeding areas in Douglas-fir stands are the recent clearcuts. Excessive use on some clearcuts has delayed or even prevented reforestation. There has been similar improvement of quality of the deer range on logged areas of western Washington (Brown 1961).

As a habitat improvement practice for deer and turkey, clearings are planned so that they complement natural openings or timber-sale cuttings. The objective on some National Forests is to have up to 5 percent of the area in dispersed openings of 1 to 5 acres.

In the Northeastern States, abandoned logging roads are seeded and maintained as grouse feeding areas as well as to facilitate foot travel by hunters. Rights-of-way for pipelines and powerlines are also utilized as clearings for wild life.

Studies of forage under various levels of tree thinning indicate that production is inversely related to the basal area of pine stands; the relationship is usually logarithmic. In eastern Washington, the degree of thinning in overstory pine timber directly influenced the vegetation (McConnell and Smith 1965). As the canopy was progressively opened by thinnings, the proportion of grasses increased linearly. Thinnings to a 40- to 45-percent canopy resulted in equal increases of both grasses and forbs.

Forb increase predominated when the canopy exceeded the 40- to 45-percent level. Browse was slower in responding to overstory thinnings.

However, digestibility of forage was not directly related to the basal area of overstory ponderosa pine in Arizona (Pearson 1964). Terminal parts of the forage were consistently more digestible.

Mechanical Treatment of Brushland.—In parts of the country—notably in California and the desert Southwest—dense brushland types over wide areas are literally impassable to big-game animals. Control of dense chaparral serves to provide space for animal movement as well as to increase the abundance and nutritional quality of low-growing forage. Type conversions in the chaparral are often justified as multi-functional projects. In California, many of the projects have been carried out to create fuel breaks to facilitate fire control, to improve watershed conditions, and to increase forage for livestock and wildlife.

Taber (1953) determined that chaparral density significantly influenced black-tailed deer reproduction. Forage quality was highest where chaparral was interspersed with herbaceous vegetation and with burned-over areas. It was poorest in mature, dense chaparral.

In Arizona, the better mixed chaparral ranges carry 20 to 30 deer per square mile. On dense chaparral, deer stocking averages 4 to 5 deer per square mile. Plant composition is the principal factor accounting for this difference; few species with lower levels of nutrition are generally found on the poorer quality ranges.

Chaining, railing, beating, and plowing are forms of mechanical treatment of brushland used to improve forage quality and the carrying capacity of the range. In Arizona, Swank (1958) found that sprouts from railed shrubs had much greater moisture content during April and July, compared with those on undisturbed sites. Growth of sprouts followed a pattern similar to that of moisture content. On railed sites, sprouts grew vigorously from early April to the middle of August, while nonrailed shrubs ceased growing in May. Use by deer and cattle coincided with high moisture content and rapid sprout growth, indicating that forage quality was definitely a factor.

In Utah, dense juniper forests with very little understory herbage have been successfully converted to productive ranges for both deer and livestock. This was done by chaining to kill the trees and then seeding (Plummer et al. 1966).

Mechanical treatment of shrubs as a range improvement practice for both deer and cattle has, perhaps, its greatest application in the desert Southwest, where competition for soil moisture is often critical. Because of relatively high costs per acre, projects usually are economically justified only when multiple benefits accrue.

Herbicide Treatment.—The use of herbicides as a tool of management affects wildlife in a number of ways. On the positive side, herbicides have been put to good use on Idaho big games ranges to top-kill tall brush and to induce basal sprouting. Wild-fire, some 60 years ago, burned vast areas of conifers; these areas were subsequently invaded by various shrub species—predominantly tall willows.

Elk herds soon responded to the new forage crop. Much of the brush has now grown beyond reach of big game and has been highlined. As a result, the carrying capacity of the range is reduced, and, unless effective measures can be applied, elk herds must be sustained at lower population levels. Trials in the use of herbicides have shown great promise in top-killing tall brush to produce succulent sprouts at the root crown.

Herbicide treatments of cattle range on Black Mesa, Colo., (Tietjen et al, 1967) have shown remarkable results in another way. Applications of 2,4-D initially reduced forb abundance by 80 to 90 percent. This was immediately followed by a similar reduction in pocket gopher populations. These gophers could not survive where their preferred food was eliminated by herbicide treatment. It was determined that common grasses provide only a marginal diet for gophers.

Another example of the adverse effect of herbicides on wildlife has been indicated in feeding studies of grouse in southeastern Idaho (Klebenow and Gray 1968). The most important food plant during the young grouse's first week of life was Harkness gilia. After the first week, common dandelion and loco made up most of the diet of young grouse. Obviously, spraying of sagebush with herbicides, which kills most of the forbs, could seriously reduce grouse production. This points up the need to reserve dispersed, untreated blocks of sage type on important grouse habitat when range improvement programs are planned.

Herbicides are often used to curb new growth of shrubs on chaparral areas previously cleared by mechanical means. Seedlings and new sprouts are vulnerable to herbicides, whereas the large, mature shrubs cannot be effectively controlled by this means.

Pruning and Hinge-Cutting.—The top-pruning of browse is a form of mechanical treatment of tall-growing shrubs used to induce growth from lateral buds. Bitterbrush, for example, exhibits the characteristic of apical dominance. It responds to top-pruning by development of lateral buds.

In southern Idaho, tall bitterbrush was topped 3 feet above the ground. Initial response was spectacular; however, the ratio of production between topped and control shrubs dropped steadily from about 9:1 in the first growing season to about 2:1 in the fourth season after topping (Ferguson and Basile, 1966). A major benefit of the topping is the nearly complete availability of the new growth. Before treatment, practically all new growth was beyond the reach of deer. Further research is needed to determine if treatment as severe as this affects longevity of the plants and if repeated removal of twig growth stimulated by pruning will maintain the increased production at a higher level.

Hinge-cutting of trees and tall shrubs benefits browsing animals. Under this practice, trees and tall shrubs are partially cut above the ground and are tipped over so that the tops are accessible for use. The partial or hinge cut permits the fallen tree to remain alive and put on new growth, all of which is accessible to browsing animals. The foliage in treetops that receives full sunlight is commonly more palatable and nutritious than lower parts. This observation is confirmed by Hoffman (1961) in his studies of winter forage of blue grouse. The partial cut also stimulates production of basal sprouts.

Hinge-cutting as a habitat improvement practice is more widely used in the Northeastern States, often in connection with wildlife clearings.

Prescribed Burning.—Some of the earliest work in prescribed burning was the evaluation of bobwhite quail production in relation to burned-over range (Stoddard 1942). The time of burning determined whether quail habitat would be improved or damaged. Unless late-winter burning was done prior to the end of February, newly sprouted legume food plants were greatly harmed.

In the South, burning removes both the old herbage of broom sedge and the accumulation of litter. It stimulates a succulent growth of various perennial legumes that are important in the quail's diet. Winter berries and fruits are also important food items. To prevent widespread loss of these important foods, a system of fire lanes may be needed to provide fire protection for some of the more productive berry-producing areas.

Field tests have also demonstrated the importance of prescribed burning on certain deer ranges. In western Oregon, a comparison of cutover and burned openings with check areas in untreated timbered range showed significant differences in deer production (Einarsen 1946). Harvested bucks on the burned range averaged 213 pounds. On the closed canopy range, bucks averaged 125 pounds. The protein content of preferred browse was consistently higher on the burned range than on the timbered range. Weight losses and mortality coincided with periods of low protein levels, which were more pronounced during extended periods of cloudy weather.

In Arizona chaparral types, protein content of browse in recent burns was found to be generally higher than that in unburned areas (Swank 1958). Browse use by both deer and cattle was much greater in the burn than on adjacent range. The favorable effects of burning were significant for 1 or 2 years, but declined in succeeding years. In California, Schultz et al. (1958) found that prescribed burning increased the nitrogen and phosphorus available to plants. Under favorable burning conditions, dense chaparral can be effectively controlled by prescribed burning; however, there is a risk that the fire may burn beyond control.

Fertilizing.—To improve wildlife habitat, the application of fertilizer to wildlife range has not been adequately tested. To date field tests have been sporadic and not completely coordinated. One of the principal drawbacks to this practice is its moderately high cost and the need for periodic followup treatments.

Washington State perhaps pioneered the large-scale use of fertilizers as a result of public pressures to divert elk use from private farmlands on the Olympic Penninsula. Starting in 1954, various fertilization trials led to the practice of applying 2 tons of oyster shell aggregate lime and 160 pounds of 10–20–20 chemical fertilizer per acre on nearby State-owned lands. When planting accompanies fertilization, the treated forage attracts elk throughout the summer, fall, and winter. On established sod, fertilizer is added in September, and elk are held throughout the following winter (Brown and Mandery 1962). Treatment every year or two is needed because of the high annual precipitation and its leaching effect.

In California, brush seedlings responded to fertilizers, but at different degrees than grasses (Schultz et al. 1958). It was found that composition could be changed by different applications of fertilizers and that one browse species could be favored over another by differential treatment. The sugar content of plants was raised by the application of phosphorus and potassium, whereas nitrogen prolonged succulence of plants.

Two soils derived from basalt and pumice and supporting bitterbrush were given fertilizer treatments to test forage response in eastern California (Wagle and Vlamis 1961). Bitterbrush plants in the basaltic soils formed root nodules and apparently had an adequate

source of nitrogen. In the pumice soil, root nodules did not form on plants, and the response to nitrogen application was pronounced.

The effects of nitrogen fertilizer on the palatability of silver fir twigs and buds to rodents were particularly significant in western Washington (Gessell and Orians 1967). Terminal shoots which had responded to nitrogen application were severely damaged by small rodents in winter. However, adjacent unfertilized trees were unaffected. The change in feeding habits resulted from a 20-percent increase in nitrogen and protein content of the damaged parts.

Plantings and Attractants.—Game food plantings serve a number of purposes; one is the augmentation of protein and the various dietary elements that may be deficient in native vegetation during part of the year (Halls and Stransky 1968). Quality forage grown as supplement may be in the form of succulent green herbage, browse, fruits, seeds, or other plant parts or forms. There is little evidence that food plantings directly increase game numbers. As attractants, however, they can increase hunter success and facilitate hunting by drawing deer or other game to these concentration points.

One objection to plantings of introduced species is their artificial appearance in the natural environment. This is particularly true of cereal crops and other exotic plants. There are opportunities, however, to use native species of high nutritional quality, and perhaps to develop strains of low to moderately palatable forage species. Selection of superior strains of juniper, sagebrush, and other browse shows considerable promise for improving game ranges.

Field studies have shown that individual native plants vary in palatability. In Washington, salal is considered unpalatable in some localities and as an important forage plant in other areas. Juniper utilization is related to the essential oil content of individual plants (Smith 1959). Preferences for sagebrush are less obvious than those for juniper. Likewise, on bitterbrush ranges, there is often wide variations in the degree of utilization among individual plants. These differences are probably inherent in the plants themselves; however, soils and other environmental factors may play a role. Selections of these and other species are being propagated and tested to a limited extent on important winter ranges.

In a detailed investigation of palatability of deer forage plants, Longhurst et al. (1968) found a generally positive correlation between palatability and digestibility. Grazing animals can and do select forage that has a much higher protein content than that of the average forage on a particular site. Deer obviously select plants with high nutrient content; however, it is unlikely that they can smell the nutrients but may be responding to compounds not yet identified. Experiments in California involving sheep with aesophageal fistulas showed that selected grasses had 15 percent protein while grass clippings had only 8 percent protein. In another California study, rumen content of deer collected in October contained an average of 17.6 percent crude protein, while clipped forage on the same area containing the same proportion of plant species had only 6.9 percent protein. Feeding studies showed very little increase in rumen protein over protein content of the forage before consumption (Bissell 1959).

Lauckhart (1962) jointly discusses the evolution of plants and animals, noting that the most successful plants have been those of low nutritional value. These have been able to retreat below the animal's threshold of malnutrition and thereby escape total destruction from overuse. Lauckhart cites a recent experience involving introduction of the legume, colutea, on pheasant habitat. The first plantings were immediately damaged by rabbits and small rodents. Under intensive rodent control, colutea became well established on a sizeable area. When rodent control was terminated, the introduced legume was totally destroyed in a relatively short time.

RESEARCH NEEDS

The foregoing is a brief summary of what we know about forage quality as a tool in wildlife management. The degree to which this knowledge is applied on the ground depends on various factors such as funding, work priorities, management objectives, and public support.

Despite the progress already made, a number of research needs are readily apparent in the field of forage quality. These include:

1. To determine if the high nutritive value of individual browse plants results from genetic characteristics or from soil or other environmental qualities. If higher nutritive value is a genetic quality, we should be collecting and planting seed from these selected plants and perhaps developing special seed orchards of the superior strains. The development of superior strains should involve high production and other desirable characteristics as well as nutritive qualities.

2. To determine if forage quality declines with age on longlived shrubby plants. If there is decline, can this trend be reversed or halted by grazing or by some other treatment? Is there a given level of forage removal that results in the highest forage quality?

3. The economic justification and management implications for wildlife clearings in tim-

ber types has not been fully confirmed (Larson 1967): What are specific guidelines on their size, density, shape, and optimum distribution? What are the impacts of clearings of various sizes on timber production, and does the release effect along the perimeter of the clearing help offset loss of timber production? How much does the clearing contribute to the success of the hunter and to the enjoyment of hunting? Does the clearing contribute to nonconsumptive wildlife uses?

4. How should fertilizers be applied to shrub ranges? Does fertilization influence plant composition and density as well as volume production, and how long does the treatment remain effective?

5. It would be desirable to be able to make forage quality evaluations in the field without the need for detailed laboratory determinations. Can we develop field techniques for determining comparative nutritive levels in plants?

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Forage Quality and Animal Production: Some Statistical Problems

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Many of the problems associated with the evaluation of forage quality and with animal production are problems in measurement. Some of the population parameters are difficult to define. When defined, they become even more difficult to measure. For our purposes, let us assume that the quality of forage is reflected in the yield of animal product, which therefore becomes a complete measure of quality.

Output per animal is determined by the factors shown in figure 1 (Barnes 1965). The nutritive value of forage is a function of chemical composition and digestibility. The nature of the product produced during digestion is important in determining the nutritive value of a forage, but it is so difficult to measure that it is seldom considered in nutritive value expressions. The rate of voluntary intake is determined by acceptability of the forage, rate of digestion and rate of passage, amount of forage available, and environmental effects on the animal. Thus, the two most important characteristics in the evaluation of forage as related to animal production are nutritive value and rate of intake.

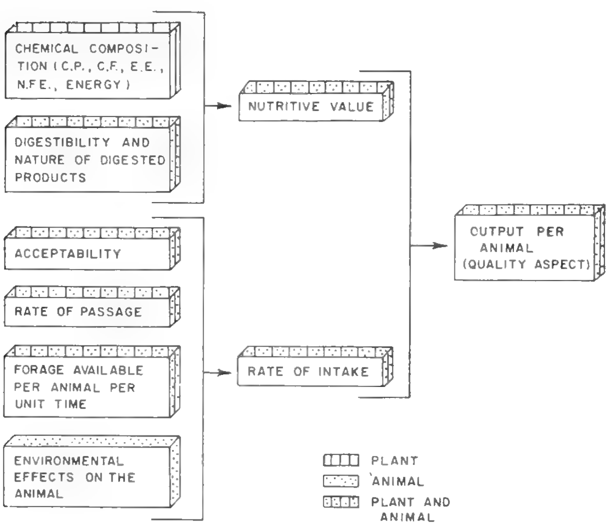

Figure 1.—The determinants of animal output (Barnes 1965).

If output per animal depends on nutrient intake, then those factors responsible for the high voluntary intake of forage are as important as the energy attributes in determining pasture quality. Since forage quality, as reflected by its rate of digestion, usually controls voluntary intake within the limits set by availability, the rate of forage digestibility is probably the most significant single nutritional attribute of any pasture (Roberts 1967). On native ranges acceptability and availability of forage may become limiting factors, particularly in some plant species. However, if that occurs, the rate of intake then approaches or reaches zero for those species.

Now let us examine briefly some problems associated with the factors already mentioned.

NUTRITIVE VALUE

Chemical Composition

It is generally agreed that net energy is the most precise measure of the value of the energy component of any forage. Net energy is the useful or available energy used for the maintenance and production requirements of the animal. Blaxter (1956) has reviewed the methods for determining net energy value. Unfortunately, net energy measurements are expensive in terms of equipment and labor, so data are accumulated slowly. Thus, people have looked for other measures, such as apparent digestibility, that can be correlated with net energy and are easier to take.

Procedures for determining the chemical constituents of forages are fairly well standardized. Where difficulties occur, they can usually be traced to improper laboratory technique (Dietz and Curnow 1966) or to poor sampling procedures. Stallcup and Davis (1965) have reviewed the numerous attempts by researchers to quantify relations between forage nutritive value and chemical constituents. Success has been limited, partly because of the inadequacy of classical chemical fractionation schemes to measure nutritive entities (nutritionally ideal chemical fractions). Another problem has been the use of empirical statistical models that do not consider basic facts concerning digestive processes (Chalupa and McCullough 1967). Lucas (1962) stated that the ideal measure of forage quality should be expressed in terms that would permit the estimation of digested end products absorbed per animal per unit of time, and should be meaningful to all kinds of forage-consuming animals under all environmental conditions. He then derived a steady-state deterministic model

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that related fecal output of nutrients per unit of feed consumed to feed composition.

Digestibility

The measure of digestibility commonly used is apparent digestibility, which is calculated by the formula, [(forage consumed − fecal output)/forage consumed] × 100. This can be expressed as a percentage digestibility of dry matter, organic matter, or energy.

The standard procedure for estimating forage quality has been the conventional *in vivo* digestibility trial. However, such trials are time consuming, expensive, and require large amounts of forage. Therefore, replication becomes a limiting factor. Once again, people looked for other methods; consequently, the *in vitro* rumen fermentation and nylon bag techniques were developed.

Increasing attention is now being paid to herbage digestibility, particularly since the two-stage rumen liquor-acid pepsin *in vitro* technique was introduced by Tilley and Terry (1963). Researchers then calculated various regression equations relating digestibility to a number of other factors. However, regression equations for *in vivo* digestibility on nitrogen, crude fiber, or lignin content have standard errors that generally are too high to detect interspecies differences (Milford and Minson 1966). A review by Barnes (1965) comparing several *in vitro* methods showed that the two-stage technique of Tilley and Terry is probably the most accurate technique for predicting *in vivo* digestibility, but precision is still a problem.

An *in vivo* technique utilizing a nylon bag in the rumen has been reviewed recently by Harris et al. (1967). Essentially, the method consists of suspending a finely ground forage sample contained in a nylon bag in the rumen for varying incubation periods (usually 24 hours). Estimates of cellulose digestibility of range forages were found by California investigators to be slightly but consistently higher than those obtained by the *in vitro* technique. Several investigators have reported nonsignificant correlations between nylon bag estimates of dry matter and cellulose digestibility and digestibility determined by total collection methods. The nylon bag technique appears to be more accurate but more variable than the *in vitro* technique for evaluating forage digestibility (Van Dyne and Weir 1964).

With further refinement, both of these "microdigestion" techniques seem to be promising. Some investigators, however, have apparently overlooked several disturbing questions:

1. Is the behavior of the fistulated animals the same as that of the intact animals grazing the same range?
2. For the *in vitro* technique, are the inocula obtained from donor animals the same as those in intact animals grazing the same range?
3. For both techniques, are the forage samples used *in vitro* and in nylon bags the same as the forage being consumed by the grazing animals?

These two techniques definitely do not solve the animal replication problem. However, it is possible that increased precision can be obtained by using the nylon bag or *in vitro* technique.

RATE OF INTAKE

We will not attempt to break down the other major function of forage quality, rate of intake, into its components because the emphasis in research on digestibility has caused work on intake to be neglected, except for a few cases. Thus, we do not know very much about some of the factors involved in the intake rate.

Workers at Macdonald College in Canada have developed a Nutritive Value Index, which is the product of digestibility and intake (Crampton et al. 1960). They found that Nutritive Value Indices show correlations with body weight changes ranging from 0.88 to 0.94. Intake and digestibility contributions to the numerical value of the index were roughly 70 and 30 percent, respectively. The same people (Donefer et al. 1966) later predicted both digestibility and intake from *in vitro* determinations that reflected rate of digestion rather than total digestibility.

The use of indigestible external indicators for measuring dry matter intake has been studied extensively. Although chromic oxide has seemed the most promising external indicator, the excretion of chromic oxide has large intra- and inter-day variations and large between-cow variations. These, then, limit the practical use of this method for determining intake. Intake measurements based on the Cr_2O_3 technique with free-grazing animals should be limited to comparative measures over short periods and the average of several animals, rather than attempting to determine accurate data for individual animals (McCullough 1959).

Other techniques have also been developed for measuring forage intake. Hyder et al. (1966) relate mean air temperature, moisture content of food, and water drunk to dry matter intake. Estimates by the water-intake method were less variable than those obtained by herbage clipping. However in this case and others, it is impossible to determine the accuracy in approximating the herbage eaten by cattle on pasture.

STATISTICAL CONSIDERATIONS

The measurement of forage quality, however defined, presents a major problem in tech-

niques. In a mixed-species stand, nutritive values are not necessarily the same for all species at any given time, and are constantly changing with time. Mixtures of the same species in varying proportions often will show interacting values as reflected in the animal response. A single-species stand involves less complexities, but still presents many problems such as changes within and between growing seasons, differences due to locality, and genetic differences in individuals.

In many livestock studies, changes in animal weights have been used to measure response to treatment. While the main source of error for output per animal is the between-animal component, overall error could be reduced if more accurate estimates of true animal weights could be obtained. A scale that automatically weighs cattle as they go to and from a water supply has been developed by Martin et al. (1967). Thus, automatic weighing of livestock may reduce overall error both by providing many more weights during the growing season, and by eliminating the weight losses due to fasting the animals prior to weighing, the conventional system now in use.

If we try to relate forage values to animal products, it seems that the real statistical problem is one of returning to specifics. In other words, we are talking about treatment populations of individual animals or very small groups of animals being grazed on small areas. For some studies it might even imply the clipping or mowing of the vegetation and subsequent feeding to animals in pens or stalls. Digestibility could then be determined by total collection methods. From small sample tests, we could then devise sensible treatments that would change forage values. Then we could try them on larger areas.

Experimental designs utilizing individual animals or small groups of animals that are confined or grazing small areas are available. Many of these designs have been reviewed by Federer (1955). Some recent papers include those by Stobbs and Joblin (1966a, 1966b), who discuss an "animal" Latin-square design and variable stocking-rate designs, and by Gardner and Centeno (1966), who discuss the removal of the effects of uneven grazing in pasture experiments.

On native and seeded western ranges, it seems that the problem of forage quality evaluation can be resolved if the following questions are answered.

1. How far can we go in using the methods and designs developed for pasture research in more humid regions? An answer to this question should be the first step.

2. Can we develop new methods and techniques for use on western or forested ranges? For vegetation-oriented studies, an answer could be possible through further research and development of electronic or radioisotope, or even through laser instrumentation. For animal-oriented studies, the picture seems cloudier. However, we should intensify our efforts on such studies.

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FACTORS INFLUENCING FORAGE QUALITY

Environmental Influences on Nutritional Value of Forage Plants

WILLIAM A. LAYCOCK[1] and DONALD A. PRICE[2]

INTRODUCTION

Environmental conditions such as weather, soil, plant competition, and grazing can directly or indirectly affect the nutritive value of plants for grazing animals. The most obvious direct effect is leaching of nutrients from plants by rain. Many environmental conditions affect the chemical composition of plants indirectly, often by causing changes in the form or in the phenological development of plants. The study of these effects is complex because single factors rarely act alone; most changes in the nutritive status of a plant are caused by numerous, interrelated factors whose effects often cannot be separated. Even when the effect of a single factor can be isolated, the mechanism of the change in composition of a plant may be very complex. These interactions must be remembered in any evaluation of plant nutrient content and forage value.

WEATHER

Precipitation: Leaching

The amount and distribution of precipitation affect chemical composition of plants both directly and indirectly. The direct effect, which will be discussed in this section, is leaching of nutrients from herbage. The indirect effect, which is caused by variations in the amount of soil moisture available for plant growth, will be treated in the "Soils" section.

Leaching of mature or dry herbaceous plants as a result of exposure to rain often results in large decreases in protein, phosphorus, ash, and carotene. Crude fiber and lignin are not leached and thus increase in percentage as leaching progresses (Guilbert et al. 1931;. Guilbert and Mead 1931; Watkins 1937, 1943.

Not all species react in the same way to leaching. Watkins (1937, 1943) found that calcium content in various range grasses was significantly reduced by heavy winter precipitation in New Mexico, while Savage and Heller (1947) found that calcium content of grasses in Oklahoma was little influenced by leaching. Crude protein of bur clover in California was little affected by leaching (Guilbert and Mead 1931), but crude protein content of native grasses in New Mexico was greatly reduced by leaching (Watkins 1943).

For animal nutrition, leaching of nutrients from dry or mature herbage is probably most significant; however, leaching of considerable amounts of nutrients from actively growing plants by rain, mist, or dew also occurs. A review by Tukey (1966) of research on leaching of metabolites from aboveground plant parts listed 15 elements and inorganic compounds, 8 carbohydrates, 23 amino acids, and 15 organic acids that have been identified from plant leachates (table 1). Many constituents important to plant growth and animal nutrition are affected by leaching: Calcium, iron, manganese, nitrogen, phosphorus, potassium, and various carbohydrates. Because of this leaching in the field, chemical composition of plants grown in the greenhouse cannot be considered representative of the chemical composition of the same plants grown in the field.

The amount leached from leaves depends on several environmental influences and upon the condition of the plant. Young leaves are less susceptible to leaching than are older leaves. Injury to leaves by frost, disease, insects, or mechanical means increases leaching loss. In undamaged living cells differentially permeable membranes bar free movement of material out of the cells. When these membranes are injured, their differentially permeable characteristics are destroyed; thus, there is greater movement of metabolites out of the cells when

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TABLE 1.—*Metabolites leached from plant foliage (Tukey 1966)*

	Organic		
Inorganic	Carbohydrates	Amino acids	Organic acids
Boron	Fructose	Alanine	Aconitic
Calcium	Galactans	Arginine	Adipic
Chlorine	Glucose	Asparagine	Ascorbic
Copper	Lactose	Aspartic	Citric
Iron	Pectic substances	β-alanine	Fumaric
Magnesium	Raffinose	Cysteine	Glutaric
Nitrogen	Sucrose	γ-aminobutyric	Glycolic
Phosphorus	Sugar alcohols	Glutamine	Lactic
Potassium		Glycine	Maleic
Silica compounds		Histidine	Malic
Sodium		Hydroxyproline	Malonic
Strontium		Isoleucine	Pyruvic
Sulfur		Leucine	Succinic
Zinc		Lysine	Tartaric
		Methionine	Acidic glycosides
		Phenylalanine	
		Proline	
		Serine	
		Threonine	
		Tryptophan	
		Tyrosine	
		Valine	

they are in contact with leaching solutions (Tukey and Morgan 1963). Therefore, leaching might be more pronounced from grazed plants than from ungrazed plants. Frosts followed by rain also might increase leaching losses and thus reduce the nutritive value of range plants.

Intensity and volume of rain affect degree of leaching. A light drizzle over a long period removes considerably more nutrients than an intense storm does. Dew is an effective leaching agent, especially in seasons and climates where rainfall is low. Other factors that influence leaching are light, temperature, and the nutritional status of the plant.

Temperature

Temperature is important in determining rate of development, phenology, and total yield of many plants, thus indirectly influencing chemical composition. However, effects of temperature are often confounded with effects of rainfall and other influences. It is clear that high temperatures are generally detrimental to plant growth, but distinguishing response to temperature from response to a moisture deficiency caused by the high temperature is difficult (Laude 1964).

In herbaceous plants in active growth or in the flowering stage, an increase in air or soil temperature up to 80°F. often increases the nitrogen (protein) content in the foliage. In growth chamber studies, Brown (1939) and Bowman and Law (1964) determined that the percentage of protein of grasses increased as temperatures increased from 60° or 65° to 80°F. Similar increases in percentages of nitrogen in the foliage of various plants, caused by increases in soil temperatures up to 80°F., were reported by Nielsen et al. (1960a, 1960b). These increases may have been at least partly related to morphological changes in plants. In some studies grasses were reported to have a higher leaf-to-stem ratio at higher temperatures. Leaves of grasses usually contain more protein than stems (Cook et al. 1959); thus, more leafy plants would be expected to have higher protein content.

Increases in percentage of phosphorus in foliage with increased soil temperature were reported by Nielsen et al. (1960b, 1961) and Levesque and Ketcheson (1963). However, increased temperature does not cause increases in nitrogen and phosphorus in all species. Nielsen and Cunningham (1964) found that the content of these nutrients in Italian ryegrass was little affected by temperature.

The response of other nutrients to temperature is quite variable. A decline in content of nitrogen-free extract with increasing temperature was reported by Brown (1939), and declines in lignin and cellulose content with increasing temperatures were reported by Bowman and Law (1964). Brown (1939) found ash content little affected by temperature.

Mellin et al. (1962) found that protein content and digestibility of timothy, which normally decreased in June as plants approached maturity, increased somewhat after a week of low temperatures and above-normal rainfall. However, this change was probably due to in-

creased soil moisture and to a delay in maturity rather than to temperature. In New Mexico, Watkins (1943) found that in mild winters with above-normal precipitation, range grasses had higher carotene content than in colder, drier winters. Presumably, this content was higher because the basal leaves and stems of the grasses remained green as a result of favorable temperature and moisture.

LIGHT INTENSITY

Lack of adequate light has definite effects on plants; some effects are direct, but most are indirect. Plants growing in the shade usually have the following characteristics compared to those of the same species growing in the sun:

1. Less herbage production (Cooper 1960; McConnell and Smith 1965; Pace 1958; and VanDyne and Heady 1965a).
2. Lower percentage of nitrogen-free extract (McEwen and Dietz 1965) or total carbohydrates including reducing sugars, invert sugars, and easily hydrolyzable carbohydrates (Watkins 1940; Welton and Morris 1928).
3. Higher percentage of lignin (Anonymous 1959; VanDyne and Heady 1965b).
4. Higher percentage of protein (McEwen and Dietz 1965; Roberts 1926).

Most of these differences are only indirectly caused by shade. Stage of development is often retarded in shaded areas (McEwen and Dietz 1965), and soil moisture is higher in shaded areas (Cook and Harris 1950); therefore, shaded plants remain succulent longer during the summer.[3] Since protein and moisture content have a high positive correlation (Campbell and Cassady 1954), higher moisture content of plants is probably responsible for the presence of more protein in shaded plants. Reduced leaching because of intercept of rain by overstory species might also be a factor.

Even the effect of shade on total production is not clear in all studies. Welton and Morris (1928) found that artificial shading had the same effect as tree cover in reducing carbohydrate content of grasses, but artificial shading did not reduce total yield because there was no competition for soil moisture from the tree species. However, in other studies under controlled conditions, reduced light levels have decreased production of some species (Leopold 1964). However, shade-tolerant species may be affected very little by low light intensities.

[3] Krueger, William C. Lignin, protein, and sugar relationships of plants on different soils of California's north coast. M.S. thesis, Humboldt State Coll., Arcata, Calif.

SOIL

A great many studies have shown that plants of the same species grown in different soils often differ in chemical composition and, consequently, in palatability (Heady 1964). Even when the causes of differences in soil were defined, other influences may have been acting in conjunction with those defined, or were confounded with them. Beeson (1941) stated this very clearly:

> "While plants are dependent upon the soil for their mineral nutrients, climatic conditions so affect . . . physiological processes that the composition of both the mineral and the organic matter of crops may be greatly modified even though the crops are grown upon identical soils. . . . Plant composition is modified by both the climate and the soil in which it is growing, and both these factors are closely interrelated, often modifying the effect of the other. Thus the assimilation of phosphorus growing in calcareous soils may be less in dry than in wet years, whereas entirely contrary results may be obtained in plants growing in siliceous soil. . . . Crops growing in the same soil type separated by sufficient distance so as to not receive the same amount of rainfall at the same time in any one year may be quite different in their chemical composition."

Various soil factors that affect chemical composition are discussed below.

Soil Moisture

The amount of soil moisture available for plant growth affects both the yield and chemical composition of plants. However, in most studies of plant composition, effects of soil moisture are confounded with temperature, stage of plant maturity, and many other factors. Early in the growing season soil moisture is often abundant and most herbaceous plants are green and growing rapidly; the moisture, protein, phosphorus, and carotene content of such plants generally is high, whereas the fiber, lignin, and nitrogen-free extract content is low. During the middle and latter part of the growing season in temperate regions with a continental climate, precipitation and soil moisture decrease, temperature increases, and herbaceous plants grow to maturity and become dry. As these events occur, the following changes take place in most herbaceous plants:

1. Percentages of protein and phosphorus

decrease (Cook and Harris 1950; Oelberg 1956; and many others).

2. Percentage of carotene decreases (Atkeson et al. 1937; Whitman et al. 1951).

3. Percentages of nitrogen-free extract and crude fiber (Savage and Heller 1947) or lignin (Gordon and Sampson 1939) increase.

4. Digestibility of most plant constituents decreases (Cook et al. 1961; and others).

5. Percentage of tannin increases in plants that contain this compound (Donnelly 1959).

Most of these changes result from plant maturity and are only indirectly affected by the decrease in soil moisture. However, early drying of soil under drought conditions makes plants dry or mature earlier, which, in turn, hastens the seasonal changes in chemical composition. The decrease in protein as soil moisture becomes deficient is at least partly caused by a breakdown of protein occurring as leaves wilt (Thompson and Morris 1966). Late summer or fall rains replenish soil moisture and cause green regrowth of plants, which is more nutritious to animals than the dry herbage (Atkeson et al. 1937; Mellin et al. 1962; Savage and Heller 1947; and Skovlin 1967).

Soil moisture and stage of growth affect ether extract, ash, and calcium content in various ways, depending on species and location. In some species percentages of ether extract and ash decrease as soil moisture decreases and as plants mature (Cook and Harris 1950; and Savage and Heller 1947). However, the trend is less regular than for protein or phosphorus (McClean and Tisdale 1960), and no change occurs in some species (Cook and Harris 1950, 1952).

Calcium content of grasses has been reported to decrease during drought (Ferguson 1931). However, Orr (1929) found that irrigation caused little change in calcium content. Increases in calcium with increase in maturity of grasses were reported by Orr (1929), Daniel and Harper (1934), and Pritchard et al. (1964). Savage and Heller (1947) found no correlation between stage of growth, time of year, or precipitation and calcium content of grasses, but found that calcium increased in forbs as plants matured. Many other examples of varying reaction of calcium to moisture could be cited.

Chemical composition of leaves of deciduous shrubs often follows the trends just described for grasses and forbs during the growing season. However, chemical composition of some shrubs may not be strongly affected by summer drought or season because shrubs often have deeper root systems and thus are assured of more soil volume from which to draw moisture (Oelberg 1956). In Idaho, Blaisdell et al. (1952) found that protein and phosphorus in the leaves of sagebrush and other shrubs decreased only slightly during the summer and that the shrubs contained more of these nutrients than the grasses and forbs in the fall.

Soil Depth

Cook (1959) studied the chemical composition of seeded grasses on deep, sandy loam soils and shallow, rocky, clay loam soils in Utah. Plants on the shallow soil (1) contained more protein and ash and less lignin and cellulose and (2) were more palatable to livestock than the plants on the deeper soil. However, soil depth was only indirectly responsible for this difference; plants on the shallow soil were more leafy and had smaller stems than those on the deep soils. The leafy characteristic probably explains the higher palatability and generally better nutritive quality of the plants on the shallow soils. Digestibility of the plants was not studied, but it would probably be higher on the shallow soil because of the lower lignin content.

Stoddart (1941) compared the chemical composition of *Symphoricarpos rotundifolius* on three soils of different depths in Utah. Plants on the deeper soils had more ash and phosphorus than those on shallower soils, but about the same amounts of other nutrients. The contradictory results of this study and the one cited by Cook were probably due to site differences not measured, such as soil nutrients or moisture.

Nutrient Content of the Soil

Many studies show that the nutrient status of plants is directly affected by the nutrient content of the soils. This is most clearly shown in studies of the effect of fertilizer on chemical composition. This subject will be treated in another paper, so only a few references will be included here.

Midgely (1937) concluded that an abundance of available plant nutrients in soil is reflected in the chemical composition of the plants. However, this relationship does not exist for all soils and all species, and the effect of the nutrient status of the soil may be changed or modified by other factors. For example, Cook and Harris (1950) found that plants growing in aspen stands contained more protein and phosphorus than those grown in sagebrush stands, even though many of the sagebrush soils contained more nitrogen and more phosphorus than the aspen soils. Increased shade and higher soil moisture content in the aspen stands were believed responsible for the differences.

Daniel (1934) and Daniel and Harper (1934) found only a slight relation between

the amount of calcium and phosphorus in the soil and the amount in prairie grasses growing on the soil. They concluded that plants normally low in calcium and phosphorus remain low even when grown in fertile soils, and that plants normally high in these elements remain high even when grown in poor soils.

Parent Material and Texture of Soil

Parent material can affect the chemical composition of plants only indirectly through the derived soils. Acidity, nutrient status, texture, and water-holding capacity of soil may be different in soils developed from different parent materials. Few studies have been made of the effect of parent material on plant composition. In Massachusetts, Archibald and Bennett (1933) found that limestone soils produced plants with higher calcium content than other parent materials. In South Dakota, McEwen and Dietz (1965) found that plants growing on limestone soils had higher ash, moisture, and protein content during vegetative growth than similar plants growing on soils derived from metamorphic rocks. However, factors besides parent material and soil influenced these differences; the limestone sites were at higher elevations and had higher precipitation. Consequently, the stage of plant maturity was retarded and soil moisture was higher than on the metamorphic sites. No difference between parent materials was found for nitrogen-free extract, crude fiber, crude fat, calcium, and phosphorus content of plants.

Texture of soil can influence chemical composition of plants—mainly through its effect on water-holding characteristics and nutrient status. Finer soils have a higher nutrient exchange capacity and can hold more water (Midgely 1937). However, little agreement has been found during studies comparing chemical composition of plants on soils of different textures. Archibald and Bennett (1933) reported that loams and sandy loams with a compact substratum had good water-holding capacities and produced herbage higher in protein and calcium and lower in crude fiber than excessively drained sandy loam soils. Grizzard (1935) found that alfalfa plants grown in fine soils such as clay loams had a higher nitrogen content than plants grown in coarse, sandier soils. Clarke and Tisdale (1945) found that plants grown in sand were lower in phosphorus content than those grown in loam, but that the content of other constituents was not affected by texture. Thus, the differences in results of these studies were probably caused by factors other than soil texture.

Compaction of soil can also affect the nutrient status of plants, but little research on this has been reported. VanDiest (1962) found that the nitrogen content of corn grown in compacted soil was significantly less than that of plants grown in less compacted soil. Content of phosphorus and potassium in plants was not affected by soil compaction.

ALTITUDE

Altitude affects plant composition through the interrelation of light intensity, carbon dioxide concentration, temperature, precipitation, and length of growing season (Oelberg 1956). Development of plants is often delayed and precipitation is often greater at higher elevation (McEwen and Dietz 1965). Therefore, plants at different elevations compared at a given time reflect composition differences due to variations in development and in soil moisture as well as the other factors mentioned above. In Wyoming, Roberts (1926) and McCreary (1927) found that crude protein, phosphorus, and nitrogen-free extract increased with altitude whereas crude fiber decreased.

GRAZING

Grazing can affect the chemical composition of individual plants by altering the form of growth or the progress of development of existing plants. The chemical composition of available forage as a whole is affected when grazing changes the composition of the plant community. Plants of different species, growth forms, or stages of development often have markedly different nutritive content and digestibility.

In discussing grazing effects, we will be considering both the specific nutrient content of a plant or species and the actual diet or effective nutrition of the grazing animal, as determined by grazing habits and the nature of the forage.

Effect of Herbage Removal on Plant Production and Nutrient Content

Many studies have shown that removal of herbage, if too severe or too prolonged, will reduce dry-matter yield of forage. However, such clipping treatments may increase the nutritive value of forage. Protein, phosphorus, and other desirable nutrients decrease as plants mature, and lignin and other nondigestible components increase. Herbage removal by grazing or clipping interrupts development of plants, prevents maturity, and prolongs growth or initiates regrowth. The composition of clipped plants is similar to that of plants in an early growth stage; the percentages of protein, phosphorus, and carotene are high, and the percentages of crude fiber or lignin are low (Fudge and Fraps 1944; Jameson 1963; and Stoddart 1946). Di-

gestibility of nutrients in clipped plants also remains high (Mellin et al. 1962).

In some pasture plants the increase in protein percentage in clipped plants is great enough and prolonged enough to result in a greater total yield of protein in clipped than in unclipped plants even though clipping reduces total herbage yield. Jameson (1963) concluded that ". . . cutting treatments are less detrimental to protein yields than to dry matter yields. If the cutting treatment does not have a severe effect on dry matter, protein yield is often increased."

On arid ranges clipping may not increase total protein content of many plants if soil moisture is limited. Aldous (1930) found that native prairiegrasses clipped at 2-week intervals had lower dry-matter production but higher protein content than unclipped plants. This decrease in yield of herbage produced a decrease in actual quantity of protein despite the higher percentage of protein. Blaisdell et al. (1952) found that despite decreases in percentages of protein and phosphorus in unclipped bluebunch wheatgrass and arrowleaf balsamroot plants as the season advanced, total quantities of these constituents increased in the plants because of the relatively large increase in the total amount of herbage.

In evaluating how changes caused by grazing affect the diet of animals, digestibility as well as amount of protein must also be considered because digestibility of protein generally decreases as plants mature (Blaser 1964; Cook et al. 1961; Staples et al. 1951; and many others). The class of grazing animal must also be considered. Some studies have shown that sheep digest protein more efficiently than cattle (Cook and Harris 1968; and Forbes 1950).

Response of shrubs to browsing or clipping is similar to that of herbaceous plants. Removal of leaves and twigs during the growing season generally stimulates new twig growth that is higher in moisture content, phosphorus, protein, calcium, and ash and lower in crude fiber than undisturbed twigs (Reynolds and Sampson 1943). However, if plants are browsed too closely, they may eventually die (Leopold 1950; Reynolds and Sampson 1943).

However, the higher protein content in young twigs does not necessarily mean that young twigs furnish more protein to the animal. According to Bissel and Strong (1955) the high moisture content of young twigs results in less protein and other energy-containing materials per unit of material eaten than when plants are eaten later in the season or during the dormant period. However, the digestibility and the percentage and total amount of protein during the two periods would have to be known to determine the effect of the differences in protein content on the nutrition of the animal.

Effect of Range Condition and Nutrition of Livestock

Range managers often assume that a decline in range condition results in a decline in nutritive value of the available forage plants. In some cases this decline does occur. Esplin et al. (1937) found that annuals and other species that invaded overgrazed desert ranges in Utah were less palatable, less nutritious, and less dependable as a source of forage than the native climax plants. However, in another study in Utah, Goebel and Cook (1960) found that good forage species on desert ranges were higher in cellulose and other carbohydrates but lower in ether extract, protein, calcium, and phosphorus than poor species. They concluded that improvement of range condition will not always result in a higher nutrient content of the forage.

In other studies on desert ranges in Utah, Cook et al. (1962, 1965) have shown that the overall nutrient content of herbage on ranges depends on the species present. If poor ranges have a predominance of shrubs, the diet of sheep will be high in protein, ash, lignin, and ether extract. If palatable grasses predominate on any range, diets will be high in cellulose, other carbohydrates, and metabolizable energy.

Even if chemical composition of plants on good and poor ranges does not greatly differ, herbage production, and thus total nutrient production, usually are lower on poor ranges. In this situation, livestock are often forced to consume more of the less nutritious and often less digestible portions of plants (stems, leaf bases, etc.) than they do on good ranges (Cook et al. 1954, 1962; Piper et al. 1959). Cook et al. (1953) found that as degree of utilization increased, lignin increased and the amount and digestibility of desirable nutrients (protein, phosphorus, and cellulose) and the gross energy decreased.

Effect of Selectivity on Diet

Animals are highly selective in regard to the species and parts of plants they eat; therefore, the botanical composition of a range or pasture alone is not a good indication of diet. For example, on California annual range, sheep fitted with esophageal fistulas consistently consumed forage that was higher in protein and lower in crude fiber than samples clipped from the same pasture (Weir and Torell 1959). The same relationship was found for the diet of steers by Smith et al. (1959) and by Hardison et al. (1954).

Even chemical analysis of whole plants

known to be eaten by animals does not give adequate indication of the nutritive content of the diet. Sheep and cattle prefer leaves and tender stems and reject the more fibrous, coarser stems. Consequently, the forage eaten is of much better quality than chemical analyses of the entire plant would indicate (Cook et al. 1948; Weir and Torell 1959). In general, protein, phosphorus, cellulose, and gross energy are higher in the parts consumed than in the total current growth.

Where forage is plentiful, selectivity enables animals to maintain nutrient levels of their diet relatively constant even though the nutritive value of the plants decreases with maturity. This maintenance of level of nutrition has been found on pure stands of crested wheatgrass (Cook and Harris 1952) and on mixed stands of grasses and shrubs (Cook et al. 1962; Edelfsen et al. 1960). If utilization becomes heavy enough, animals can no longer be so selective, and the nutritive level and the digestibility of the diet may eventually decrease. This decrease is often less pronounced or occurs later than the corresponding decrease in the nutritive value of the entire plant. Arnold (1962) found that the digestibility of forage selected by grazing sheep on phalaris-subterranean clover pastures in Australia did not decline until almost 3 weeks after a substantial decline in digestibility of the same species clipped and fed to penned sheep. If animals switch to less palatable but highly nutritious species, such as some of the shrubs, when utilization of the palatable plants becomes heavy, the nutritive content and digestibility of the diet may increase with increased degree of utilization (Cook et al. 1962).

COMPETITION

The presence or absence of competition from other species evidently can affect the chemical composition of plants. However, carefully controlled studies to determine exactly what changes are caused by competition have not been conducted. In California, VanDyne (1965) found wide differences among the morphology, chemical composition, and digestibility of annuals grown in pure stand plots and among the same species collected from rangelands. The areas compared presumably were on the same type of soil, but the pure stands were seeded on areas where other grasses had been grown. Thus, some of the differences in composition obtained may have resulted from site, soil, or microclimatic differences as well as from competition. VanDyne found that many grasses on the range had a greater percentage of weight in stems and leaves and less weight in heads than the same species in pure stands. For the brome species this resulted in a higher overall protein content for the range plants than for those in the pure stands. *Avena barbata* plants from the pure stands contained more protein and less silica than range plants. Brome plants from the pure stands had higher silica content. Ether extract was higher in range plants for all species. Other constituents were quite variable, and 50-percent differences were not uncommon. VanDyne concluded that chemical composition and digestibility of plants from pure-stand plots cannot be used to make inferences about nutritive value of these plants under range conditions.

The presence of plants with nodules containing nitrogen-fixing bacteria can increase the nitrogen content of the soil and thereby increase the yields of other plants. Burton et al. (1953) found that Coastal Bermuda grass in Georgia produced three times as much hay per acre when bitter blue lupine was seeded into the sod and when the mature growth was subsequently disked into the sod as similar stands of grass without lupine. Lawrence (1958) found that fallen leaves of young alder in Alaska, which has nitrogen-fixing nodules, added as much as 140 pounds of nitrogen to the soil per acre each year. As a result of the increased fertility, growth of associated species was stimulated. No data on chemical composition of foliage was presented in either study. However, available nitrogen in the soil is the major influence on nitrogen content of herbage (Whitehead 1966); consequently, it might be speculated that the increased nitrogen in the soil in both instances increased the protein content of the foliage of the plants associated with the nitrogen-fixing species.

Dietz et al. (1962) found that sagebrush samples collected from the Poudre range in Colorado were lower in protein, ash, calcium, and phosphorus than samples collected from the Mesa Verde area in southern Colorado. The Poudre site had a mixed stand of sagebrush, grasses, forbs, and bitterbrush on south-facing hillsides. The Mesa Verde site was an alluvial fan that supported an almost pure stand of sagebrush. The higher nutritive value of sagebrush at Mesa Verde was attributed to less competition from other vegetation and to better soil conditions. However, the two areas are widely separated, and differences in climate or other factors could have caused the difference in composition.

CONCLUSIONS

In almost all studies reported, the effects of individual environmental factors were confounded with other influences or with stages of plant development. Carefully controlled field and growth-chamber studies are needed to define the effects of environmental factors, both alone and in combination, on the chemical com-

position of forage plants. In any study, the possible effects of leaching and of the presence or absence of competing species and the measurable environmental factors must be considered. Information from such studies would enable range managers to predict the effect of specific environmental changes on the nutritive value of native plants. It would also permit intelligent selection for seeding of species best suited to furnish needed nutrients to animals in areas where the range of environmental factors is known.

SUMMARY

Weather, soil, competition, and grazing are highly interrelated factors influencing the chemical composition and nutritive value of plants for grazing animals. Many of these factors affect the chemical composition of plants indirectly by hastening or delaying plant development. The percentages of many desirable components such as protein, phosphorus, and carotene are high when plants are young. As plants mature, the percentages of these components decrease and less digestible components such as crude fiber, lignin, and nitrogen-free extract increase. In temperate climates these changes associated with plant maturity occur concurrently with an increase in temperature and a decrease in soil moisture during the growing season. Below-normal precipitation that causes deficient soil moisture hastens these seasonal changes; cool, rainy weather may prolong or reinitiate the green, nutritious stages of growth.

Precipitation may also have a more direct effect by leaching nutrients from plants. Protein, phosphorus, ash, and carotene are often leached from dry mature plants, leaving the indigestible crude fiber or lignin. Leaching can also take place in younger, actively growing plants; the amount leached depends on age of leaves, damage, amount and duration of rain, light, temperature, and nutrient status of the plant.

In many plants, percentages of protein and phosphorus increase as soil or air temperature increases up to 80°F. The effect of temperature on other nutrients is variable and differs among species.

Shaded plants generally produce less herbage and have less total carbohydrates and nitrogen-free extract than plants grown in full sunlight; however, they usually have more protein and lignin. Some of these differences are not caused directly by the shade; however, shaded areas generally have higher soil moisture, and plants grown under shade are often retarded in stage of development and are more succulent than sun-grown plants.

The depth, texture, and nutrient status of the soil influence the chemical composition of plants, but these factors are closely interrelated with both climate and plant form. Plants grown under conditions of soil and climate that lead to more leafy growth form will generally be more nutritious because the content of protein, phosphorus, and other desirable nutrients is higher in leaves than in stems. Protein, phosphorus, and nitrogen-free extract of plants have been found to increase with altitude, but some of these differences probably result from higher precipitation and a delay in stage of development at higher elevations.

Grazing affects the nutrient content of plants by altering plant form or state of development. It may also change the nutrient status of the whole plant community by changing the species composition of the community. A decline in range condition often, but not always, results in a decline in nutritive value of available forage. Less palatable species that may predominate on ranges in poor condition may be more nutritious than some of the more palatable plants. For most species, removal of herbage by grazing often reduces the yield of dry matter. However, such treatment may increase protein, phosphorus, and other desirable nutrients because it delays maturity and prolongs growth or initiates regrowth if soil moisture is adequate. If the clipping does not have a severe effect on dry-matter production, total protein yield may be increased. However, on arid ranges, clipping in midgrowth may reduce yield but may yet not initiate regrowth because of limited soil moisture.

The botanical composition of a range is not a good indicator of either botanical or chemical composition of diet of livestock because animals are highly selective as to the species and parts of plants eaten. This selectivity often enables animals to hold the nutrient level of their diet relatively constant during periods when the nutritive value and digestibility of plants are decreasing.

The chemical composition of plants may be affected by associated species. Plants grown in pure stands may differ in form, chemical composition, and digestibility from the same plants grown in mixed stands. Plants with nitrogen-fixing bacteria in nodules may increase the nitrogen content of the soil and thereby increase both the amount and protein content of the herbage produced.

In most of the studies reported, effects of individual environmental factors were confounded with those of other influences or with stages of plant development. Carefully controlled studies are needed to define the effects of these factors, both alone and in combinations, on the chemical composition of forage plants.

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Comparative Nutritive Values of Forage Species[1]

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INTRODUCTION

The game food resource in any type of game range has never been scientifically managed. Nevertheless, to reach this objective, two main courses of action are being pursued. One course consists largely of the application of results of years of management experience, bolstered by the application of research findings (for example, nutrient content of deer forage species) when they show promise of solving immediate management problems. The greatest obstacle to progress is the excessively long period of cut-and-try methods needed to determine which practices have more than a local application. This course progresses by regular revision of short-term management plans.

The second course consists of a process of experimental research that draws largely on available basic information on forage species and animal nutrition. The determination of nutritive values of forage species is one of the tasks within this research process. As the subject of this paper, this task should be placed in perspective within the research process.

The process begins with a record of the distribution and abundance of plant species on a unit of game range. Other kinds of required information are needed in about the following order: A list of forage species made up from evidence of use by the game species of interest; the parts of each forage species used by this game species; amounts of these diet components seasonally available on the unit of range; seasonal dietary habits and the nutritional requirements of the game species of interest; seasonal nutritive value of forage species; methods of forage production; and, a system of forage management that can produce a reasonably stable yield of game for recreational use. The present paper is concerned entirely with methods of nutritive evaluation of deer forage that are needed to perform a specific task within the research process already described.

[1] This manuscript is published with the approval of the Pennsylvania Agricultural Experiment Station as article 3540 in the journal series.

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NUTRIENT CONTENT OF FORAGE

Much work has been done in analysis of most of the nutrient elements of forage for deer. What follow are examples of the variety of unrelated pieces of information; from these attempts are made to piece together workable plans for deer management.

Chemical analysis of woody browse of several species revealed the occurrence of a monthly variation in the nutrient content of the previous year's growth (Hellmers 1940). The chemical composition of browse plants was found to be influenced by the effects of forest fires (Dewitt and Darby 1955). The time and freshness of cutting were shown to influence the chemical composition and the acceptability to deer of twigs from felled hardwood trees (Alkon 1961). Seasonal changes reportedly occurred in the protein and phosphorus content of "portions of the current growth of twigs" in Arizona browse plants (Swank 1956). And the results of chemical analysis of "portions of plants normally eaten by deer" led to the conclusion that differences in chemical composition did not adequately explain the division of species into palatable and nonpalatable groups (Gastler et al. 1951).

From studies conducted in western Oregon, it was shown that there was a relation between the crude protein content of browse and deer size (Einarson 1946), but it was not stated which part of the browse plants was analyzed. A study was made of the influence of soil type on the "available nutrients" in current annual growth of selected deer-browse species (Hundley 1959). Seasonal differences in proximate composition were much greater than differences due to soil type.

In all these reports, the authors have interpreted differences in chemical composition to be related to differences in nutritive value. Such data may be qualitatively useful for assessment of the general direction of range-management practice; however, consideration of some fundamental principles of ruminant nutrition obviates their usefulness for quantitative estimation of the carrying capacity of deer range.

First, single species never constitute the entire diet of wild deer, and the nutritive value of any diet component depends upon its relationship with all other foodstuffs in the diet. Also, analysis of entire plants or of "current year's growth" produces values that may be entirely unrelated to either the nutritive qual-

ity of the particular plant parts eaten by the deer or to their potential contribution toward balancing the mixed diet. The futility of nutritive evaluation of single browse species is shown by the results of a Michigan study in which aspen and cedar browse were compared in digestion trials with deer (Ullrey et al. 1964). Deer-management experience had indicated that aspen was heavily utilized. However, aspen proved a starvation diet, as indicated by severe weight loss and negative digestion coefficients, due to low feed intake during the digestion trials. However, it is reasonable to assume that aspen is an important dietary component, if it is consumed as part of a complete diet.

DIGESTIBILITY

Digestion trials were conducted in which various browse species were fed to deer along with alfalfa of known digestibility and in which their relative digestibilites were measured by difference (Dietz *et al.* 1962). This method theoretically should produce more meaningful results than single-species trials; however, discrepancies between predicted and actual digestion coefficients reported by these workers raised questions as to whether even this method produced results that are worth the laborious collection of large amounts of browse, which when collected may not be representative of that eaten by free-ranging deer.

Animal nutritionists have for more than 100 years been searching for methods of predicting feed values from simple laboratory analyses. Their progress has been reviewed (Van Soest 1964). This same author pointed out the importance of finding methods which will predict, in addition to the digestibility of feeds, their acceptability or level of voluntary consumption.

Various methods of evaluating forages for wild ruminants were reviewed (Short 1966). The advantages of small-scale laboratory tests were indicated; these include *in vitro* digestibility measurements which utilize inocula from the rumens of freshly killed wild animals or from fistulated captive animals. Advantages of such methods which require only a few grams of forage are obvious, if they can be shown to give results that are closely related to actual nutritive values. The relative merits of *in vivo* and *in vitro* forage evaluation methods are more thoroughly discussed in other papers in these meetings.

Many workers have studied relationships between chemical composition and digestibility of forage. Also, various small-scale *in vitro* digestion techniques, involving exposure of forage samples to fermentation by rumen micro-organisms, have been tested (Oh et al. 1966). Following a comparison of these methods, it was concluded that several choices are available for comparing digestibilities of forages within a species, including simple crude protein analysis, but that the twostage *in vitro* digestible dry matter method of Tilley and Terry (1963) was the method of choice to predict the digestibility of all forage species and mixtures of species. Other workers have studied the use of small-sample *in vivo* techniques; here the samples are suspended in the rumen of fistulated animals, and the rate of disintegration of the feed is observed (Lusk et al. 1962). These methods (*in vitro and in vivo*) have the advantage of measuring the digestibility of the feed in a biological environment representing ruminal conditions of a healthy animal consuming a complete diet.

SMALL-SAMPLE TECHNIQUES IN FORAGE EVALUATION

Studies are underway in the Department of Animal Science, Pennsylvania State University, University Park, Pa., to compare various criteria of feeding value, in order to select a small-sample technique which will yield value that are reasonably well correlated with actual feeding values as measured in digestion trials. It is likely that, for purposes of estimating the deer-carrying capacity of a given unit of deer range, most of the parameters (number of animals, yield of forage, portions utilized, etc.) entering into the final computation must be at best relatively rough estimates; therefore, determination of feeding values of the many edible materials with a high degree of precision would be wasted effort. In this respect, our needs differ from those of livestock and dairy researchers who are working toward maximum efficiency of production and therefore, we need research methods that will accurately measure small differences in feeding value so that rations for known numbers of animals, or even individuals, can be concocted and fed in proper amounts and proportions for most efficient and competitive production. Even after more than a century of research involving many hundreds of workers, the ideal method has not been found, and there is still disagreement as to which method is best.

The Penn State Forage Testing Service's functions are to analyze samples of forages (hays and silages) sent in by dairymen and livestock producers and to recommend supplemental feeding practices for more efficient production (Adams et al. 1964). This Service uses relationships among crude protein (CP), crude fiber (CF), and total digestible nutrients (TDN) content to calculate feeding values. Based upon data available from more than 700 forages on which TDN has actually been deter-

mined by digestion trials, the equations used by this agency differ according to the type of forage studied as follows:

Legume Forage:

$$\text{TDN} = 74.43 + 0.35\ \text{CP} - 0.73\ \text{CF}$$

Grass Forage:

$$\text{TDN} = 50.41 + 1.04\ \text{CP} - 0.07\ \text{CF}$$

Mixed Hay Crop Forage:

$$\text{TDN} = 65.14 + 0.45\ \text{CP} - 0.38\ \text{CF}$$

The current studies on deer forage are concerned with the application of these or similarly developed equations in the estimation of nutritive values of browse and other deer foods. Calibration of such experimental evaluation techniques requires actual measurement of digestibility of many different samples of browse and other deer food. Therefore, sheep are used as test animals because of the obvious advantages of using domesticated animals for such studies. Similarities of the digestive capacities of sheep and deer have been demonstrated and will be discussed later. Deer of sufficient uniformity and docility for use in digestion trials are rare.

To avoid difficulties such as those encountered by Ullrey *et al.* (1964) in feeding single species of browse in digestion trials, browse materials fed in these studies will be mixed with complete diets of known digestibility, and their digestibility will be determined by difference.

A minimum of such laborious conventional digestion trials will be conducted; the number will be that needed to establish a sound relationship between actual digestibility values and those determined by various small-sample techniques such as the *in vivo* nylon bag technique and the *in vitro* digestion methods of Tilley and Terry (1963). One of these small-sample methods may then be selected for calibration of a still more simple and practical chemical analysis.

CRUTE PROTEIN AS AN INDEX TO FEEDING VALUE

It is well established that forage crops grown for feeding domestic animals have their highest feeding value at the rapidly growing stage. At this stage, crude protein and mineral content is highest, and the energy of the carbohydrate portions of the plant are most readily available to the animal. Lignification of cell wall structures has not progressed sufficiently to limit their accessibility to the digestive action of rumen microbes. In general, then, a high crude protein content is considered a desirable attribute in a forage only partly because of the need for protein in the diet for growth and other metabolic functions. It is also desirable because high-protein forages are usually succulent and palatable and because their nonprotein (carbohydrate) constituents are highly digestible. Also, the high content of nitrogen and minerals in such forages permits the maintenance of a healthy, vigorous population of rumen microbes. Consequently, the animal has the capacity to digest more fibrous foods, which may at times constitute a relatively large portion of the diet of the deer. Thus, even if the high-protein forage is available in relatively small amounts, it may make a valuable contribution to the diet by serving to supplement other foods. Such foods, if eaten alone, would be so indigestible as to constitute a starvation diet.

Emphasis on the importance of the crude protein content as an index of feeding value of forages does not mean that the importance of an adequate supply of available (digestible) energy should be overlooked or minimized. Much more nutriment is required to maintain the normal energy metabolism of livestock than for all other purposes combined; and if this need is satisfied, probably all other requirements will be incidentally covered (Swift 1957). However, when considering forages and browse-type foods, the availability of their energy, and the amounts consumed, are closely related to such factors as stage of maturity and succulence. Such factors are in turn associated with nitrogen (crude protein) content in such a way as to give relatively high positive correlations between nitrogen content and digestibility of energy. Thus, it may be safe to predict that if the combination of natural foods eaten by a deer contains an adequate percentage of crude protein, other nutritional requirements probably will be incidentally covered. In most browse forage species, crude protein is negatively correlated with crude fiber content (cell wall constituents). Therefore, equations similar to those used in forage evaluation for domestic animals should provide convenient and sufficiently accurate means of computing feeding values of foods sampled from a given range.

A deer's diet is usually varied, and studies of food preference may not just reflect differences in palatability of various foods but also instinctive efforts to balance the ration. A simplified, hypothetical model of this situation is illustrated by the use of selected data from sources fully described later in this paper. These data indicate that black cherry browse is about twice as rich in crude protein as red maple browse (fig. 1). In this theoretical situation, we will assume that only these two spe-

cies are available to a deer, and that the animal consumes a diet consisting of 30 percent black cherry browsed to 2 inches beyond the bud (average crude protein content 16 percent, fig. 1) and 70 percent red maple. Each 30 pounds of black cherry would provide 4.8 pounds of crude protein. To provide 100 pounds of a mixed cherry-maple diet containing 9 percent crude protein, the 70 pounds of red maple would have to supply 4.2 pounds of crude protein; this would require that its average crude protein content be about 6 percent. According to figure 2, this could be achieved if the deer browsed red maple to a length of about 9 inches beyond the bud.

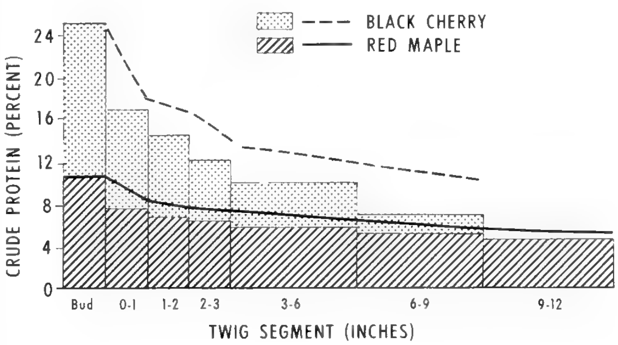

FIGURE 1.—Crude protein content of red maple and black cherry terminal twigs during the dormant season (Camp Run area). Bars represent the mean crude protein content of each segment; the line represents the weighted mean of whole browse from bud to length clipped. The black cherry was in the Camp Run area, and the red maple was in the old-field area.

This is a grossly oversimplified example of how only one factor (crude protein content) may influence the determination of what the deer eats. It is not intended to suggest that the deer has a built-in computer that enables him to select from his greatly varied "smorgasbord" of available foods an accurately balanced combination of diet ingredients. However, it may suggest that a properly planned and coordinated program of research may result in the eventual accumulation of a more-or-less complete "matrix" of data. Such a matrix may cover most of the important deer foods, experimentally determined feeding "standards" or requirements of deer, increased knowledge of their eating habits and behavior, factors influencing availability and utilization of their foods, and conceivably a more-or-less "computerized" solution of forage-management problems. It is recognized that the problems are exceedingly complex, that they are different for each unit of game range, and that precise solutions and applications will never be possible.

CRUDE PROTEIN CONTENT OF TWIGS

The habit of deer in feeding to consume only a portion of a plant part is well known. The development of a methodology in deer-forage evaluation requires knowledge of the nutrient content of that portion. But the task of defining the portion, or even the plant parts in some species, has not been completed for any unit of deer range. The difficulty of the task is increased by the variation that occurs in the size or the amount of the portion consumed. An example is twig browse.

A study [4] was conducted to determine the crude protein content of twigs because of the possible use of crude protein in a forage evaluation method. Also, because the portion of twigs browsed by deer has not been defined for most woody species, there was a special interest in determining the general pattern of protein distribution in twigs. It was also of interest to compare crude protein content between browse species and within species by season, structural parts of the plants, and origin of plant growth.

Methods

Twigs of three native browse species—black cherry, red maple, and American beech—were collected on the Allegheny National Forest, Pa. The sample material was clipped from the current annual growth of unbrowsed plants growing under several conditions. All twigs were sectioned into various lengths, ovendried at 105° C., and weighed.

Twigs were collected from about 20 black cherry and red maple seedlings growing under similar conditions of treatment in an old field area. All were wildlings, 5 feet or less in height, that had been transplanted with a 3 by 3 foot spacing to the old field 6 years previously and fenced for a study of the response of seedlings to simulated deer browsing. The sample material was collected from March 31 to April 2, during part of the dormant season.

In another case, black cherry terminal and lateral twigs were collected from several hundred seedlings, 1 to 4.5 feet in height, growing in each of four clearcut blocks in widely separated areas. Collection was made during the dormant season in January and April, and again during the growing season in June. Through error, the leaves from the twigs collected in the growing season were not saved for analysis. The twigs were succulent and buds has not yet formed on these seedlings.

The terminal twigs of sprouts from 30 to 50

[4] A cooperative study between the College of Agriculture, The Pennsylvania State University, and the Northeastern Forest Experiment Station, Forest Service, USDA.

black cherry stumps were collected in June in each of three widely separated clearcut areas. A 3-inch section of the succulent terminal twig was clipped, and the leaves were removed. In most instances, the entire sprout was less than 3 inches in length. Two of the areas were in the first growing season since cutting, and the third area was in the second growing season.

In another instance, terminal twigs were collected from branches at the apex and at the sides of freshly felled pole-size black cherry trees. Collections were made in February in four different poletimber stands. At least two trees were felled in each of three locations in each stand.

In the final instance, a section was clipped from the terminal twigs of stump sprouts and root sprouts of beech. Collections were made in January in four different areas in which cutting had been done several years prior to the collection of sample twigs.

Results and Discussion

Black cherry and red maple twigs obviously differed appreciably in crude protein content, and in the rate of decline in this value with distance from the bud (table 1). There was little difference in crude protein content between terminal and lateral twigs within species; however, there was a pattern of consistent small difference between comparable twig sections. It seems unlikely that this could account for the frequently observed preference by deer for terminal twigs.

The crude protein content of black cherry terminal twigs from the four clearcut areas suggested that differences due to the date of collection within the dormant season might be more important than those due to geographical location, despite the confounding of season with location (table 2). There was little difference in twigs collected in January from the Klondike and Mill Creek areas, and only a slight difference in twigs collected in April from the Chappel Fork and Camp Run areas. However, there was a great difference in crude

TABLE 1.—*Crude protein content of twigs clipped from black cherry and red maple seedlings growing in an old field area, March 31–April 2, 1966*

Twig section	Black cherry		Red maple	
	Terminal	Lateral	Terminal	Lateral
Inches	*Percent*	*Percent*	*Percent*	*Percent*
Bud	19.69	20.06	10.31	9.69
0–1	13.44	12.88	7.81	7.13
1–2	10.81	10.31	6.94	6.56
2–3	10.00	8.94	6.44	6.00
3–6	7.69	7.19	5.81	5.44
6–9	6.31	5.44	5.06	4.81
9–12	5.38	4.44	4.69	4.50

TABLE 2.—*Crude protein content of terminal twigs of dormant black cherry seedlings growing in five different areas on the Allegheny National Forest*

Twig section	Area and collection date(s)				
	Klondike, 1/17–1/19	Mill Creek, 1/25–1/26	Old Field, 3/31	Chappel Fork, 4/19	Camp Run, 4/20
Inches	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
Bud	13.38	14.38	19.69	23.69	25.03
0–1	9.88	10.19	13.44	14.88	16.63
1–2	8.69	8.69	10.81	11.86	14.60
2–3	8.00	7.63	10.00	10.56	12.00
3–6	6.94	6.50	7.69	9.63	9.88
6–9	5.94	5.56	6.31	7.25	7.61

protein content between terminal twigs collected in January and those collected in April. The data for black cherry terminals in table 1 are also shown in table 2 as other evidence of the possible influence of date of clipping on crude protein content.

A comparison of twigs from black cherry seedlings in the four clearcut areas (table 3) shows that there was very little difference in crude protein content between the Klondike and Mill Creek areas. Collections in both places were made in January. Values from the Chappel Fork and Camp Run areas, where the collections were made in April, indicate that the crude protein content of twigs increased with the approach of the growing season, with perhaps a further suggestion that lateral twigs in the Chappel Fork area may have been slightly slower to respond than terminal twigs.

A comparison of twig locations for black cherry collected during the growing season is prevented by the confounding of the effects of site and date of collection. However, there appeared to be a gradual decrease in crude protein content within comparable twig sections in all four areas with the progress of the growing season, even though collections were made within a 2-week period (table 4). The diminution of crude protein levels probably indicates its translocation to the leaves during this period. The data in tables 3 and 4 suggest a need for more detailed studies of the effect of season on composition and nutritive value of browse.

Stump sprouts of black cherry collected from three areas on June 21, 23, and 29 contained a higher level of crude protein (19.38, 20.56, and 25.69 percent, respectively) than did comparable sections of black cherry seedlings (table 4). The differences due to the effect of origin of plant growth probably mask the effect due to site difference.

The crude protein content of twigs from the apex and sides of felled black cherry trees was approximately the same. Most differences between similar sections (buds and 0-3 inch) of

TABLE 3.—*Crude protein content of terminal and lateral twigs of dormant black cherry seedlings growing in four different areas on the Allegheny National Forest, Pa., 1966*

Area	Buds		0–3 inch		3–6 inch	
	Terminal	Lateral	Terminal	Lateral	Terminal	Lateral
	Percent	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
Klondike	13.38	13.44	8.86	8.25	6.94	-----
Mill Creek	14.38	13.69	8.84	7.69	6.50	-----
Chappel Fork	23.69	14.63	12.43	10.32	9.63	-----
Camp Run	25.03	25.31	14.41	12.51	9.88	-----

TABLE 4.—*Crude protein content of terminal and lateral twigs collected during the growing season from black cherry seedlings on four different areas of the Allegheny National Forest, Pa., by date of collection, 1966*

Date of collection	Area	Terminal		Lateral	
		0–3″	3–6″	0–3″	3–6″
		Percent	*Percent*	*Percent*	*Percent*
June 13	Camp Run	13.81	8.06	11.80	7.69
June 14	Chappel Fork	11.38	7.63	11.80	7.75
June 21	Klondike	12.06	7.50	9.63	6.44
June 27	Mill Creek	10.63	6.50	7.31	5.25

the apex and side twigs did not exceed 1 percent among 12 samples for each twig section. Crude protein values were about the same as those found in the seedling twigs collected in January. The reported high preference by deer for apex twigs of felled trees apparently cannot be explained solely by differences in the level of crude protein. As with all other dormant black cherry twigs, the crude protein level from the bud to the adjacent twig section sharply declined.

In general, there was very little difference between corresponding twig sections of stump or root sprouts of beech. And there were only slight differences in crude protein levels between the bud and 0–3 inch section. The range in protein content for all beech samples was 6.00 to 7.56 percent. Beech is generally regarded as a very low-preference deer browse, although the frequency of use of beech is high on the Allegheny National Forest, Pa. But this high use may be related to its relative abundance and to consistently high deer populations dating back to the 1930's.

DIGESTIVE CAPACITIES OF DEER AND SHEEP

In another phase of the present studies, the relative digestive capacities of deer and sheep were compared to determine the extent to which existing knowledge of domestic ruminant nutrition and forage evaluation might be applied to the deer, and to investigate the feasibility of using sheep as experimental animals to evaluate deer foods.

The two species were compared in conventional digestion trials, using total collection of feces, and a technique in which 2-gram samples of forage or browse were suspended in the rumen through a permanent fistula in closely woven nylon bags, and disappearance of cellulose from the bags in 48 hours was used as a relative measure of digestibility.

For the conventional digestion trial, two wether sheep were housed in metabolism cages previously described (Bratzler 1951), and two yearling castrate deer were housed in cages also previously described (Cowan *et al.* 1968). One deer and one sheep were fitted with permanent rumen fistulae, which allowed the nylon bag technique to be used simultaneously with the total collection method. All animals were fed chopped, firstcutting timothy hay that had been harvested after emergence of heads before bloom; it contained 10.2 percent crude protein and 34.7 percent cellulose on the air-dry basis. Feces were collected for 10 days, following a 7-day preliminary period on the same level of feed intake.

Cellulose was determined on feed and feces by a modification of the method of Crampton and Maynard (Lusk et al. 1962). Crude protein was determined by a modification of the Kjeldahl method, and energy by means of an Emerson Bomb Calorimeter. The results of the test indicate that deer and sheep exhibit similar digestive capacities for the nutrients measured (table 5).

As a further test of the similarity of the digestive capacities of deer and sheep, the rate of passage of the timothy hay through the digestive tract of the fistulated deer and sheep was determined. This was accomplished by dyeing with basic fuchsin, a portion of one meal of the timothy hay fed in the conventional digestion trial, and then observing the time of appearance of the dyed particles in the feces. Details of this study will be reported elsewhere, but curves are presented here as substantiating evidence that deer and sheep are similar in digestive function (fig. 2).

The number of hours required for the following was:

	Deer	*Sheep*
Time for initial appearance (i.e., time to traverse omasum, abomasum, and intestines).	14.0	16.0
Time in rumen and reticulum.	33.4	35.3
Mean time for passage of one meal.	47.4	51.3
R value (mean retention time of stained particles).	44.0	48.0

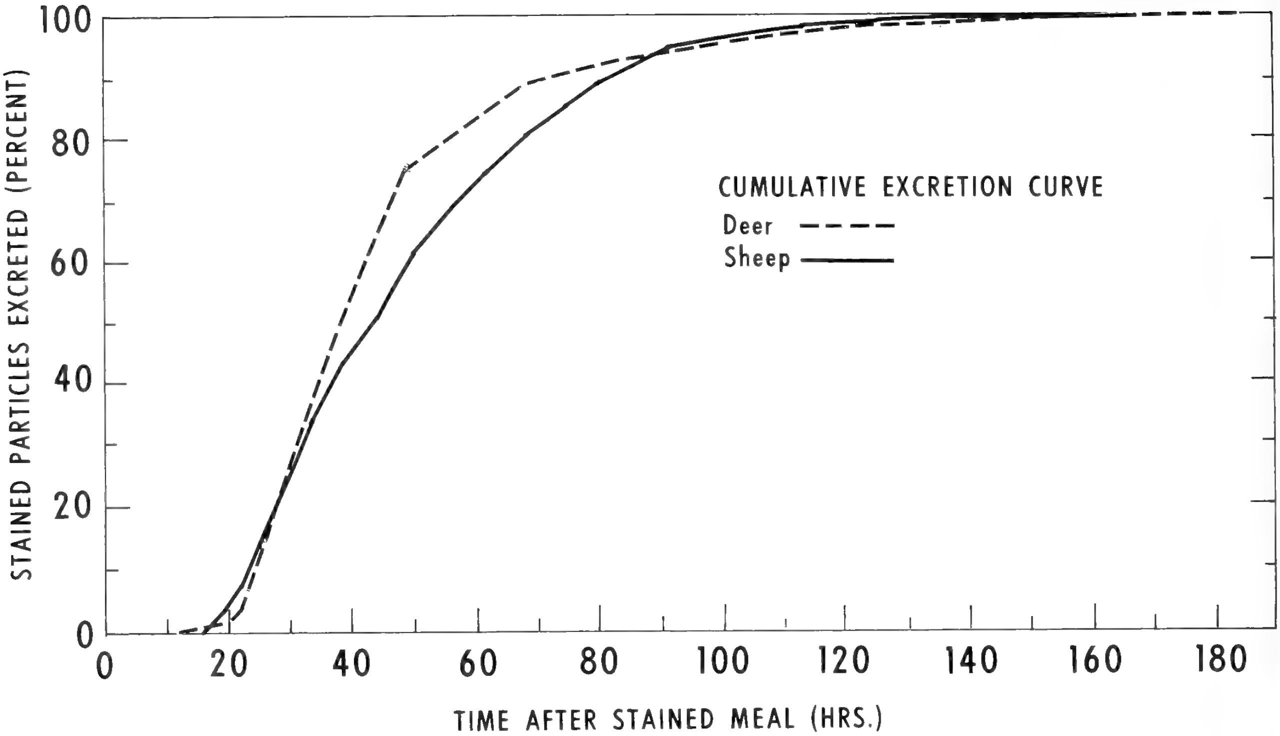

FIGURE 2.—Cumulative excretion by deer and sheep of timothy hay stained with basic fuchsin and introduced directly into the rumen via fistula.

TABLE 5.—*Apparent digestibility of timothy hay in experimental deer and sheep, measured by total collection*

Item	Fistulated deer	Control deer	Fistulated sheep	Control sheep
	Percent	*Percent*	*Percent*	*Percent*
Cellulose	56.8	55.6	54.6	55.6
Crude protein	56.0	45.0	52.9	58.9
Energy	54.5	52.0	53.8	56.1

During the same trial, the nylon bag method was used simultaneously to compare cellulose digestion in the two fistulated animals. The method used was a modification of that of Lusk et al. (1962). The timothy in the bags was from the same lot as that fed in the digestion trial, but was ground to pass through a 20-mesh screen. Other bags contained alfalfa from the same lot as that studied in a previous trial in which digestibility of ground alfalfa and wheat straw was determined when the deer and sheep were fed alfalfa pellets. It is apparent from the results of this test that digestibility measured by this method varies considerably with the diet of the animal, but that the ruminal media of deer and sheep on the same diet provide similar ability to digest cellulose (table 6). Of interest, the cellulose of alfalfa was more readily digested by both animals when the diet was timothy than when the diet was alfalfa.

It is recognized that in these studies only one forage was used to test these similarities, and that between-species differences may be somewhat greater with browse diets; however, in view of statements made previously as to the limited need for precision in evaluation of deer foods, it is felt that relative feeding values determined with sheep may be safely used in reference to deer. Also, until further experiments have more accurately delineated comparative differences between these species, it may be assumed that most of the general knowledge in the area of ruminant nutrition and nutritive values of ruminant feeds may be applied in deer nutrition.

TABLE 6.—*Cellulose digestion in sample items in experimental deer and sheep on three diets, using the nylon bag method*

	Sample item					
	Alfalfa		Straw		Timothy	
Diet	Deer	Sheep	Deer	Sheep	Deer	Sheep
	Percent		*Percent*		*Percent*	
Alfalfa pellets	48.3	50.0	30.9	32.9	----	----
Timothy hay	75.0	70.0	----	----	63.4	60.0
Natural browse	60.7	----	----	----	51.7	----

The relative digestibilities of the cellulose of alfalfa and timothy, determined when the fistulated deer was on a diet of natural food in another phase of the study, are also shown in table 6. In that phase, the deer was allowed to roam freely and to eat *ad libitum* in the woodlot surrounding the deer pens. This phase was begun in the fall when much leafy browse was available, and continued until after frost, when some acorns had fallen. Alfalfa hay was made available to supplement the diminishing supply of browse after frost. Nylon bag samples of red maple and black cherry browse, and of the alfalfa and timothy mentioned above, were suspended in the rumen for 48-hour digestion periods. Two trials were run on each forage, in separate series, so that several days elapsed between duplicate trials on a given sample. Values in table 7 represent means of the duplicate trials. It is apparent from the results (table 7) that in both species of browse the percentage of cellulose digestion is directly related to the percentage of crude protein, and is inversely related to cellulose content.

TABLE 7.—*Composition and digestibility of browse samples, using the nylon bag method, and with deer on a natural diet*

Item	Twig section	Crude protein	Cellulose	Cellulose digested
	Inches	*Percent*	*Percent*	*Percent*
Red maple	1–2	6.72	30.3	49.2
Do	2–3	6.06	31.2	43.6
Do	3–6	5.65	37.1	30.4
Do	6–9	4.94	41.1	17.8
Do	9–12	4.62	41.8	17.0
Black cherry	Bud	17.38	13.7	52.3
Do	0–1	14.40	21.0	34.0
Do	1–2	11.74	27.2	31.1
Do	2–3	10.21	30.0	27.1
Do	3–6	7.45	32.7	19.3
Do	6–9	5.86	37.4	16.3
Do	9–12	4.91	41.3	13.2
Timothy hay	-----	-----	-----	51.7
Alfalfa hay	-----	-----	-----	60.7

SUMMARY

Determination of the nutritive values of forage species is only one task in a research process that can lead to scientific management of the game food resource on a unit of game range.

Available literature relating to nutrient composition of deer forage species reveals a lack of data from which to determine relationships useful in computing or predicting nutritive value or carrying capacity of deer range units.

Reports of studies of the digestibility of forage species indicate the importance of developing small-scale laboratory tests for evaluating forages used by wild ruminants. Since many forage samples are to be evaluated, the methods to be developed must permit rapid determination of the chemical characteristics of small samples which represent nutritive value (digestibility) with a reasonable degree of confidence.

Crude protein content may be an important index of the feeding value of forages. The crude protein content of black cherry and red maple browse was determined for plants growing under different conditions. Differences in crude protein content due to geographical location or to origin of growth on the plant—(terminal vs. lateral twigs) appeared to be slight. There was a rather definite pattern of distribution of crude protein in twigs, the highest level occurring in the bud, with a sharp reduction to the first 1-inch section of twig. The level declined gradually with each succeeding section of the current annual growth. The level of crude protein increased in the distal portions of dormant twigs as the growing season approached.

It was determined that the digestive capacities of sheep and deer were similar enough to justify the use of sheep to represent both animals in digestion trials that are needed to establish relationships between actual nutritive values and small-sample evaluations.

The *in vivo* nylon bag technique appears satisfactory for determining relative digestibility of forage samples, and it shows promise as an intermediate step in the calibration of other methods involving only chemical analysis of the forage.

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Effects of Fertilization on Quality of Range Forage

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The effects of fertilizers on the quality of range and pasture forage could be the subject of a sizable book. However, we will summarize only part of the pertinent literature and some current studies on the effects of inorganic fertilizers. Remember that fertilizers may affect both the quantity and the quality of forage, and that the literature does not always draw a distinction. The quality of forage growing under range conditions is affected by many interacting factors that are difficult to measure or control.

Fertilization is an important cultural practice used to change, and usually to improve, forage quality. The amount of fertilizers applied can be measured and controlled. But caution is needed in attributing any changes in forage quality directly to fertilizer alone. Considerable insight into the entire ecosystem is needed before the effects of fertilization on forage quality can be interpreted correctly.

Our review will cover: (1) changes made in forage quality by changes in the nutrient composition of range plants and (2) changes made in forage quality by changes in the botanical composition of rangelands.

CHANGES IN NUTRIENT COMPOSITION OF RANGE PLANTS

Nitrogen fertilization in the northern Great Plains is a valuable cultural practice to increase the percentage and the total yield of plant protein and, hence, to improve forage quality (Clark and Tisdale 1945; Cosper et al. 1967; Lodge 1959; Smoliak 1965). In North Dakota, fertilization of 90 pounds of nitrogen per acre for both of 2 years on a heavily grazed pasture did more to improve the condition of the forage plants than did 6 years without grazing (Rogler and Lorenz, 1957).

Nitrogen fertilization has significantly increased the protein content in prairie grasses (Burzlaff et al. 1968; Dee and Box 1967;), in seeded grasses on mountain rangelands in northeastern Utah and southeastern Idaho (Hull 1963), and in intermediate wheatgrass in the southwestern ponderosa pine zone (Lavin 1967). The protein content of nitrogen fertilized tobosa was generally 20 to 35 percent higher than that of unfertilized tobosa on flood plains in the semidesert grassland (Herbel 1963). Many of these nitrogen-fertilizer studies have shown increased succulence of forage and extended periods of green growth, as well as increased protein contents.

Nitrogen fertilization has generally increased both the percentage of protein in early-growing grasses and the total yield of protein from flood meadows (Cooper 1956; Rumberg 1963) and from high-altitude meadows (Wilehite et al., 1955).

In California annual grassland, about 160 pounds of nitrogen per acre was required to increase the percentage of nitrogen in nonleguminous plants harvested at the end of the growing season (Jones 1963; Jones and Winans 1967). If less than half that amount was used, it increased only the percentage of plant nitrogen during the vegetative stage. These studies pointed out that the percentage of nitrogen in the plant at maturity may be less with nitrogen fertilization than without fertilization—especially in high rainfall areas where the added nitrogen is used by the plant for increased growth. Total yield of protein, however, was generally higher with nitrogen fertilization.

McKell et al. (1960) reported some benefits of fertilizing annual ranges in a dry year. They found that total nitrogen contents of forage ranged from 1.32 percent with no nitrogen fertilizer application to 1.95 percent total nitrogen from plots treated with 200 pounds of nitrogen per acre. Phosphorus and sulfur fertilizers added to nitrogen caused only minor increases in the nitrogen content of the forage. Total yield of protein was 83 pounds per acre from forage on nonfertilized plots and 153 pounds per acre from forage on plots fertilized with 80 pounds of nitrogen per acre. The application of 100 pounds of nitrogen per acre brought the total protein yield up to only 186 pounds per acre; 150 pounds of nitrogen up to 188 pounds per acre; and 200 pounds of nitrogen up to 202 pounds.

Fisher and Caldwell (1959) reported a yield of 320 pounds of protein per acre from coastal bermudagrass without nitrogen fertilization and 3,635 pounds of protein per acre with 1,332 pounds per acre of nitrogen fertilizer. Ten to 40 percent more nitrogen fertilizer was required for maximum protein production than for maximum hay production. Fisher and Caldwell (1959) also concluded that phosphorus, potassium, and lime were required to maintain high-quality forage when high rates of nitrogen were applied under high rainfall conditions.

Timely use of nitrogen on adapted grasses

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can result in a crude protein yield comparable to that of a mixture of grasses and legumes. Wagner (1954) reported that the application of 240 pounds of nitrogen per acre on orchardgrass yielded a forage that contained 18.51 percent crude protein, dry basis. More than 160 pounds of nitrogen per acre applied annually to orchardgrass or tall fescue was needed to equal the season's protein production from the grass-legume mixtures. Similar results have been reported by Ramage et al. (1958). They found that during a 3-year period, orchardgrass fertilized with 400 pounds of nitrogen per acre had an average crude protein content of 19.84 percent, dry basis. Stroehlein et al. (1968) concluded that on desert grasslands of southern Arizona, forage production can be increased and forage quality improved by properly timing fertilizer applications with adequate soil moisture conditions. They reported an extension of the green feed period, increased protein, and increased production when fertilization was delayed until after the start of summer rains.

Adding sulfur to nitrogen increased the crude protein contents of annual-type vegetation in California. Walker and Williams (1963) reported that adding 132 pounds of nitrogen and 150 pounds of sulfur as ammonium sulfate increased total crude protein by 753 percent. However, Hylton et al. (1968) found that protein synthesis in shoots of Spanish clover was affected very little by sulfur deficiency.

According to Teel (1962), potassium is necessary for protein synthesis, and a deficiency of potassium limits the normal metabolic events in plant biosynthesis to the extent that certain substrates accumulate or engage in alternative reactions. Yet, Duell (1965) reported that forage plants fertilized with ammonium nitrate and lime, but without potassium, had consistently higher crude protein percentages than plants fertilized with phosphorus, potassium, nitrogen, and lime. Also, Vincent-Chandler et al. (1962) found that in grasses grown under humid tropical conditions, the percentage of crude protein dropped consistently as potassium—up to 1,600 pounds of it per acre—was added. These three studies suggest that under humid conditions, potassium added to nitrogen can increase the yield of forage and the total yield of crude protein, but the percentage of crude protein may decrease because increased plant growth has a "dilution" effect.

Fertilizers other than nitrogen have not generally affected the quality of grass herbage in the plains and mountains of the United States (Cook, 1965; Hull, 1963; Lavin, 1967; Leven and Dregne 1963).

The effects of nitrogen fertilization on the quality, and on the morphological characteristics that influence quality, of bermudagrass were measured by Prine and Burton (1956). Besides increasing the percent of protein, protein yield, and free nitrogen content, nitrogen fertilization increased plant height, stem length, length of longest leaf blade per stem, and number of internodes per stem. But the treatments also decreased the percent of leaves and percent of stems with seed heads.

Work reported by Honnas et al. (1959) showed some contrasts among blue grama, hairy grama, and sideoats grama in response to ammonium phosphate fertilizer. Blue grama and hairy grama responded favorably in leaf length, number of stems, and forage production, while in general, sideoats grama responded negatively. However, sideoats grama seed yield did increase.

Burton et al. (1956) found that the palatability of coastal bermudagrass was improved substantially by nitrogen fertilization. They noted that protein and moisture content of herbage generally increased as nitrogen—up to 1,500 pounds of it per acre—was added. Despite improved palatability, the nitrogen treatments may have toxic effects to animals because of increased nitrate concentrations in forage (Kay 1966). Any condition which slows the growth rate of forage plants but does not prevent nitrate uptake may lead to nitrate accumulation. Hence, forages high in nitrate are often found when plant growth is retarded because other nutrients are limiting growth after high nitrogen fertilization. Nitrate accumulation may also occur after drought, cool periods, or cloudy periods.

Alexander et al. (1961) found that the protein content and the digestibility of protein of coastal bermudagrass herbage was directly related to nitrogen fertilization. The protein content of the herbage was increased up to 30 percent by increasing the rate of fertilization from 50 to 100 pounds of nitrogen per acre. The total digestible nutrients increased only slightly as the nitrogen level was increased from 50 to 100 pounds per acre. But animal gains were markedly higher at the high nitrogen rate, apparently due to differences in dry matter intake, protein content, and digestibility.

Digestible protein of well-managed forages may be higher than needed for maximum animal output. But herbage from forage plants does not generally supply enough energy to maximize animal output (Blaser 1964). Nitrogen fertilization of grasses usually increases carrying capacity and animal production per acre but seldom increases outputs per animal. It also improves the protein content and the protein digestibility, but cellulose, or crude fiber content, and lignification are not generally altered. The soluble carbohydrates (sugars and starch or fructosan) in forage may decrease with added nitrogen. Thus, the digestible energy of grass forage may not be appreci-

ably altered by nitrogen fertilization (Eheart and Pratt 1942; Poulton et al. 1957). Several other workers have reported decreases in "soluble carbohydrates" in forage with nitrogen fertilization (Jones et al. 1961; Reid et al. 1966; Waite, 1958). Reductions in soluble carbohydrates with nitrogen fertilization were attributed to the increased respiration and to the utilization of soluble carbohydrates for synthesis of protein and structural materials.

CHANGES IN THE BOTANICAL COMPOSITION OF RANGELANDS

The effects of fertilization upon the botanical composition and upon the condition of rangeland plants vary with the climate, the soil, and the plants. Huffine and Elder (1960) reported greater cattle gains on fertilized than on unfertilized native grass pastures in Oklahoma. They attributed this difference to an increase in weedy plants due to fertilization. In Wyoming, Cosper et al. (1967) found that nitrogen fertilization on a deteriorated range site changed the botanical composition from forbs and shortgrass to western wheatgrass and shortgrass. Nitrogen increased the yield of forage and the percent of crude protein in the forage. Changes in forage yield were the result of changes in the botanical composition as well as increases in plant growth.

In the northern Great Plains, Rogler and Lorenz (1957) reported that a higher forage yield after nitrogen fertilization was due primarily to an increase in the percentage of western wheatgrass in the species composition. They also reported that the crude protein level was higher on fertilized than on unfertilized plots.

Lodge (1959) noted that fertilization may enable range managers to manipulate the botanical composition of native ranges. But he indicated that such manipulation, to best serve the nutritional requirements of the grazing animal, would first require more knowledge of the effects of fertilization on the nutrient status of individual plant species and on the total vegetation complex.

Climatic and soil conditions in some areas of California have made fertilization economically feasible because of increased forage yields, favorable changes in botanical composition, and increased livestock gains per acre. However, most reports in the literature deal with increases in forage yields and in beef production. And effects of fertilization on the quality of forage are often a sidelight or are not mentioned at all.

Jones and Evans (1960) described 3 years of results of fertilization and grazing on botanical composition changes in annual grassland in California. Nitrogen fertilization increased the percent of soft chess on grazed plots on native ranges for 2 of the 3 study years, but for only the first year on ungrazed plots. It increased for 2 years the percentage of soft chess on reseeded ranges that were grazed, but decreased it when not grazed. Slender wild oats and broadleaf filaree also responded favorably to nitrogen fertilization, but both decreased when grazed. Little fertilization effect could be measured in the filaree on grazed plots. Nitrogen fertilization generally decreased the abundance of clovers, while phosphorus fertilization generally increased the amount of clovers. The percentage of clovers on the resident-range, and the crimson clover on the reseeded range, decreased under grazing, while rose clover and subclover increased under grazing. Phosphorus also increased the percentage of ripgut brome on resident-range, but this increase was less on grazed than on ungrazed plots. On the reseeded range, where phosphorus was adequate, ripgut was increased by nitrogen fertilization. Grazing reduced the percentage of ripgut on both resident and reseeded ranges.

Examples of changes in forage quality resulting from changes in botanical composition by fertilization are reported in a series of articles from a long-term study of sulfur fertilization in the California foothills (Bentley et al. 1958; Green et al. 1958; Wagnon et al. 1958). In most years, the percent of legumes increased significantly more than that of grasses on ranges fertilized with 60 pounds of sulfur per acre every 3 years. Total herbage production was increased by more than 50 percent over an 8-year period. This increase resulted in substantial increases in stocking rates and in steer gains. On ranges fertilized with sulfur the abundant clovers were grazed first, and then grasses made up most of the steer diet.

Walker and Williams (1963) concluded that sulfur can be an important fertilizer element on annual-type range and can directly enhance the growth of resident grasses much more than the growth of resident forbs. However, the nitrogen needs of the grasses must first be met. This study did not include a treatment of sulfur alone.

In a preliminary report on a current study, Conrad et al. (1966) noted that clover responses to sulfur fertilization were negligible in dry years. But in favorable rainfall years, sulfur-fertilized ranges had a higher percentage of clover than nitrogen-fertilized or nonfertilized areas. In general, sulfur has increased the number and the size of legumes on annual-type ranges; nitrogen has resulted in fewer and smaller legumes but more and larger grasses than no fertilization.

From a small plot study at the San Joaquin Experimental Range in central California (results unpublished), we found that the application of sulfur encouraged legume growth, while nitrogen reduced legume growth but in-

creased growth of grasses. Treated plots were established on a uniform site. The treatments were ammonium sulfate, ammonium nitrate, and gypsum. The first season, 1965, was favorable for plant growth. On both nitrogen-treated plots, the total yields were high, but the percentage of clover was much lower than on gypsum-treated or control plots. Ammonium sulfate-treated plots (134 pounds of nitrogen per acre) yielded 7,478 pounds per acre of air-dry herbage (2.7 percent clover). Ammonium nitrate-treated plots (98 pounds of nitrogen per acre) produced 6,307 pounds (1.2 percent clover). Gypsum-treated plots (60 pounds of sulfur per acre) produced 5,549 pounds (26.0 percent clover), and control plots averaged 3,437 pounds (7.3 percent clover).

We concluded that: (1) sulfur increased the clover yield and thereby improved the forage quality, and (2) that the adverse effect of nitrogen fertilization on clover growth was the result of competition between species with different growth requirements and with different growth habits. Early-maturing species (mostly grasses) on the nitrogen-treated plots made rapid growth and exhausted soil moisture before the temperature was favorable for clover to grow rapidly. Thus, the adverse effect of nitrogen on the legumes was indirect. Clovers on the sulfur-treated plots remained green for 2 to 3 weeks after all vegetation on the nitrogen-treated plots had dried.

The second season, 1966, was a carryover year for the fertilizer. It proved to be dry and unfavorable for plant growth. Both the total herbage yield and the percentage clover were much lower than those in 1965. The two nitrogen-treated plots yielded slightly more than 2,000 pounds per acre (0.5 percent clover). Gypsum-treated plots produced about 2,000 pounds of air-dry herbage (6 percent clover). Control plots yielded about 1,200 pounds (1.3 percent clover). The results from the 2 years demonstrate how climate can affect the botanical responses from fertilization on annual-type ranges in California.

In another test, Westfall (1966) reported unusually favorable results from sulfur fertilization. For the first 2 years after fertilization, legumes on sulfur-fertilized plots made up 88 percent of the vegetation complex, compared to 17 percent on control plots and 5 percent on ammonium sulfate-treated plots. Although there were no tests of animal responses or chemical analyses of the forage, the sulfur fertilization most likely improved the quality of the forage.

The influence of sulfur in improving the quality of range forage is demonstrated by the unpublished results of a long-term grazing study at the San Joaquin Experimental Range. Sulfur fertilization combined with yearlong grazing have consistently produced more clover than unfertilized yearlong and seasonally grazed ranges. Because the grazing rate is moderate, animal responses are due more to forage quality than to forage quantity. In 1967, a very wet year, vegetation on upland sites was more than 30 percent clover, by weight, on the sulfur-fertilized units. This was more than twice the percentage yield of clover on any of the nonfertilized units. Consequently, the cows from sulfur-fertilized yearlong-grazing units were from 100 to more than 200 pounds heavier at weaning time than cows from other range units. Their calves, when weaned, were also the heaviest calves in the study.

Sulfur fertilization, by increasing legume leafage and legume seeds on some annual-plant ranges, also provides more preferred food for California quail. Glading et al. (1940) listed both seeds and leafage of several legumes as "preferred foods". Subsequent work by Duncan and Shields (1966), Shields and Duncan (1966), and Duncan (1968) shows that legume seeds and leafage are "ice cream" for California quail. Thus, changing vegetative composition by fertilization influences the diet of some wildlife as well as domestic livestock.

SUMMARY AND CONCLUSIONS

The literature reveals conflicting evidence on the effects of fertilizers on the quality of range forage. This conflict may be attributed to the wide variety of: (1) Climate and soils, (2) growth habits of plants, (3) rates and type of fertilizers, (4) stages of maturity in which the plants are harvested for analysis, (5) methods of sampling and the plant parts sampled, and (6) the descriptive units in which the results are reported. There is a definite need for more standardization of the objectives, the methods used, and the reporting of results so that comparisons can be made. Also, many of the experimental designs should provide for economic analysis.

Nitrogen has been used more extensively as a fertilizer than any other nutrient for range crops. Thus, nitrogen fertilization has probably improved the quality of range forage in more areas than any other type of fertilization. This improved quality has generally meant increased crude protein, increased succulence, and increased leaf-to-stem ratios .Even in semiarid areas, nitrogen fertilization has improved forage quality; however, forage yields may not have been increased.

Phosphorus, potassium, and sulfur fertilizers have improved the quality of range legumes and other forbs—especially in areas of high rainfall. These fertilizers have also improved the quality of range grasses in high-

rainfall areas where high rates of nitrogen fertilizers are used.

Fertilization has one more benefit for returns from rangelands. Nitrogen, phosphorus, potassium, and sulfur fertilizers have been used alone or in combinations to obtain and maintain a favorable balance of legumes, other forbs, and grasses for high-quality herbage and for extended periods of green growth.

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Objectionable Characteristics of Range Plants

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The significance of objectionable characteristics in range plants is twofold. They may cause a direct loss in animal products by poisoning or otherwise injuring livestock, or they may simply reduce the production of usable forage. Toxic properties are naturally of great concern because of the occasional dramatic livestock losses that have occurred in the past, and because of the careful management required to prevent such losses. To a much lesser degree, some species are mechanically injurious to livestock because of peculiar structural features. These seldom cause death, but can cause condition loss or prevent forage utilization. Still less obvious are the effects of certain physiological and morphological characteristics of range plants. These affect livestock only indirectly by altering both the quantity and quality of forage available for use.

Though direct loss from poisoning is most spectacular, the loss in production of usable forage is probably of much greater economic significance. Plants with objectionable features simply occupy space and utilize moisture and nutrients that could more profitably be used by valuable forage plants. They reduce the grazing capacity of the range.

We often tend to classify plant characteristics as either good or bad, but nature is not that simple. With few exceptions, we find that objectionable features have highly variable effects—they differ both with kind of livestock and with conditions under which the features are encountered. Under certain conditions some range plants can be very harmful; under different conditions these same species provide valuable forage.

For convenience, the discussion of objectionable characteristics is divided as follows: Chemical constituents, structural features, and physiological attributes. The first two can be further divided into those factors which directly damage livestock in some way, and those which simply discourage use of what might otherwise be valuable forage.

CHEMICAL CONSTITUENTS

Poisons

The purpose here is not to list all of the range plants potentially poisonous to livestock. This information can be found in numerous U.S. Department of Agriculture and State Agricultural Experiment Station publications. Rather, the major groups of chemical constituents that have been found in toxic quantities in range plants will be pointed out and examples will be given of plants in which they occur. Much of the information on toxins was obtained from Kingsbury's textbook (1964) in which he discusses all of the known poisonous plants in the United States and Canada.

Glycosides (Glucosides)

Many glycosides are nontoxic, whereas others are very toxic. They include the most widely distributed toxins found in plants. The most prominent toxic glycosides include the cyanogenics, irritant oils, coumarins, and the saponins.

Of the numerous glycosides, perhaps the cyanogenics cause the most poisoning of livestock. Though the glycoside itself is harmless, highly toxic hydrocyanic acid (HCN) is formed by hydrolysis. Hydrolysis can occur in either the plant or in the animal. Frequently, HCN forms in the plant when growth is stunted by wilting or frosting. HCN forms more readily in ruminant than in nonruminant animals; the microflora in the rumen promotes the enzymatic action that leads to hydrolysis. Death usually is rapid, occurring within a few hours.

The cyanogenic glycoside content of given plants varies with such environmental conditions as stage of growth, rainfall, fertilization, and general climate. Both speed of ingestion and speed of hydrolysis are important in determining whether poisoning will occur. The cyanide in HCN is highly reactive and capable of entering chemical changes that will prevent absorption. It is also readily excreted. The amount of nontoxic material in the digestive tract and the degree of wetness are important as dilutants to the cyanide.

Among the most valuable range plants containing cyanogenic glycosides are *Triglochin maritima* and *T. palustris*. These occur throughout the United States on marshy sites, but are usually poisonous only when growth is stunted by drought. Various *Sorghum* spp., often used as forage crops, cause livestock losses in the Central and Southern States, especially following drought or frost. HCN poisoning has occurred, particularly from use of *S. vulgare* and *S. halepense*. The sometimes poisonous properties of *Prunus* spp. are also

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attributed to cyanogenic glycosides. *P. virginiana* is considered a major poisonous species for all kinds of livestock in parts of the West (U.S.D.A., A.D. & P.R.D. 1964; Stoddart et al. 1949). Its HCN content is particularly high in early spring.

Irritant oils of glycoside origin are found in several genera of the Ranunculaceae family. *Anemone patens* and some species of *Ranunculus,* which contain highly toxic "protoanemonin," are at least suspected of causing some animal losses.

The occasional poisonous properties of *Melilotus alba* and *M. officinalis* are attributed to the glycoside "coumarin." This compound is closely related to that used in the rodenticide, "Warfarin." Losses are generally restricted to cattle feeding on spoiled sweetclover in hay or silage; such spoilage converts the nontoxic coumarin to highly toxic discoumarol.

The saponic glycosides in *Solanum* spp., *Sesbania* spp., *Linum neomexicana,* and *Agrostemma githago* have occasionally poisoned livestock. Also, the saponins found in some legumes (i.e., *Medicago satiro*) are at least suspected of contributing to bloat in ruminants (Dougherty 1956). Saponin content varies with season, stage of growth, and plant part.

Helenium hoopesi, a major poisonous plant found in the central Rocky Mountains, derives its toxicity from the glycoside, "Dugaldin." Losses are usually restricted to sheep; however, cattle have been poisoned experimentally.

Alkaloids

Alkaloids may be present in at least 5 percent of all plant species: most often they are found as soluble, organic acids. They are particularly common in the Leguminosae and Amaryllidaceae families. More than 5,000 different alkaloids have been identified. Most affect the animal's nervous system. In contrast to glycosides, the alkaloid content in a plant does not vary much with stage of growth, climate, and water availability, but it does differ appreciably in different species. Since alkaloids are usually distributed throughout the plant, every plant part may be considered poisonous to livestock.

One of the most important poisonous genera on our western ranges is *Delphinium* spp. (Huffman and Couch 1942), which derives its toxicity from the alkaloid "Delphinine." *D. barbeyi, D. nelsonii,* and *D. tricorne* often cause severe poisoning problems on cattle ranges. Some genera very poisonous to sheep also have alkaloids as their toxin; *Lupinus* spp. contain the alkaloid "Quinolizidine," and *Zigadenus* spp. contain the alkaloid "Veratramine." The malformation in lambs known as "monkey-face" is attributed to the Veratramine found in *Veratrum californicum.* Only recently, researchers found that the congenital deformity in calves known as "crooked calf," which occurs in many parts of the West, is caused by consumption of *Lupinus caudatus* and *L. sericeus* by the dam during gestation (Shupe et al. 1968).

Oxalates

Oxalates occur in plants in the form of soluble and insoluble acids and salts. The soluble oxalates of sodium and potassium are the primary offenders. Although many plants contain small amounts of soluble oxalates, few have enough to be considered poisonous. Oxalate concentrations differ appreciably with both season and location. Usually they reach a maximum in late summer and fall.

Moderate amounts of oxalates appear to be readily eliminated by livestock; however, large concentrations can result in the precipitation of oxalate crystals in the kidneys and urinary tract. Both the amount and time of ingestion are important determinants of whether toxic levels will be reached in the blood. Also, presence of other food in the stomach lessens the absorption rate and decreases the chance of poisoning.

Halogeton glomeratus is perhaps the most well-known plant that owes its toxic properties to soluble oxalates, primarily in the form of sodium salts. The same toxin in *Sarcobatus vermiculatus* also has caused substantial losses of sheep under certain conditions. It is usually considered a good forage when eaten in moderate amounts along with other forage; however, when eaten in large amounts without other forage, especially in the fall, death can result.

Resinoids

Some of the most poisonous plants in the north temperate zone contain resinoids as their toxin. Resinoids are complex compounds that share a certain physical similarity despite having diverse chemical structures. The exact chemical structure is still unknown for most resinoids. Human beings as well as all kinds of livestock are sensitive to these toxins.

Cicuta spp. is perhaps the best-known resinoid plant. Both livestock and human beings have died from eating parts of this plant, particularly the roots. They contain the resinoid "Cicutoxin," which is characterized as a highly unsaturated higher alcohol. Cicutoxin acts directly on the central nervous system, usually causing rapid death. Most cases of livestock poisoning from this species occur in the spring, when the new leaves are toxic and the ground is so soft that animals pull up and eat the roots along with the tops.

Asclepias spp. are also highly poisonous resinoid plants. The most toxic species, *A. labriformis,* can cause death when as little as 0.05

percent of the animal's weight of green plant material is consumed. Practically all species of this genus are at least partly toxic. Although several glycosides and some alkaloids have been found in these plants, their main toxicity is attributed to resinoids. Various species of *Ledum, Rhododendron,* and *Kalmia,* and *Menziesia ferruginea,* all in the Ericaceae family, contain toxic resinoids that are known to cause livestock losses.

Photosensitizing Compounds

Photosensitizing compounds occur in a few range plants. When these plants are eaten, the animals become hypersensitive to light rays over a broader part of the spectrum than in the case of ordinary sunburn. The reaction is somewhat similar to extreme sunburn in unpigmented or lightly pigmented skin not covered by a dense coat of hair. Although the photodynamic action is rarely fatal in itself, secondary effects can cause death.

Various species of *Tetradymia* are perhaps the most prominent plants causing photosensitization in livestock. Symptoms of "bighead" are usually apparent in sheep within 24 hours after toxic quantities of *Tetradymia* are eaten. Other range plants that contain photosensitizing compounds and that are potentially injurious to livestock include *Hypericum perforatum, Agave lecheguilla, Nolina texana,* and various species of *Panicum, Lantana,* and *Trifolium.*

Other Compounds

Although not specifically related to the groups just mentioned, several plants that contain toxic properties very dangerous to livestock should be mentioned here. *Quercus* spp., primarily *Q. havardi* and *J. gambeli,* can poison cattle early in the growing season if the animals eat little besides oak leaves. In this case the toxin has been identified as "Gallotannin."

Another plant with somewhat unusual toxic properties is *Pteridium aquilinum.* This species and its varieties occur almost worldwide and contain the enzyme, "Thiaminase," which adversely affects horses by breaking down thiamine, producing a thiamine deficiency. The toxic effect on ruminants is more complex, and the exact nature of the toxin has yet to be determined.

Certain legumes contain estrogenic compounds in sufficient quantities to affect the fertility of animals. For example, the estrogen "Coumestrol" has been isolated from *Trifolium repens* (Bickoff et al. 1958). Ewes grazed on *T. repens* and *Lotus corniculatus* pastures conceived 3 weeks later, and their fertility was much less than that of ewes grazed on bluegrass (Engle et al. 1957).

The polypeptides and amines found in some fungi can also poison livestock. Perhaps most prominent among these are certain fungi like *Amanita* spp., which contain toxic peptides, and *Claviceps* spp. (ergot), which contain both amines and alkaloids.

Several important range plants contain little-known or unknown toxins that can cause severe livestock losses. Foremost among these is the group of plants called locoweeds, this group consists of several different *Astragalus* and *Oxytropis* species. Most important are *A. mollissimus, A. lentiginosus, A. wootonii, A. earlei,* and *O. lambertii.* Toxins in these plants have some of the characteristics of an alkaloid. The locoweeds are one of the few plants to which livestock can become addicted. Usually locoweeds are unpalatable, but if animals are driven to eat them because of hunger, the animals begin to crave them. This craving can be fatal unless addicted animals are removed from ranges where these plants occur.

Cattle grazing *Festuca arundinaceae* pastures are sometimes afflicted with "fescue foot;" symptoms include lameness and a predisposition to dry gangrene at the extremities (Yates 1962). These symptoms are similar to those cause by ergot poisoning, but the fungi ergot is not involved. However, toxic metabolites produced by the mold *Fusarium nivale* are suspected of contributing to this disorder (Yates et al. 1968).

Hymenoxys oderata and *H. richardsonii* have killed many sheep, but the toxin they contain has not yet been identified. *Oxytenia acerosa,* which once killed many cattle in southwestern Colorado, also contains an unknown poison.

MINERALS

Mineral excesses and deficiencies in plants ordinarily are caused by soil imbalances rather than by species characteristics. However, some plants have the ability to concentrate certain minerals in their foliage, which then becomes toxic.

Selenium is very toxic to livestock. Soils relatively high in selenium occur sporadically throughout the Western United States and Canada. Selenium uptake by plants depends on a number of conditions—the most important is the amount of selenium in soluble form in the soil. The particular chemical form of the selenium and the quantity of other soil elements, such as sulphur, also influence uptake.

Certain selenium-accumulating plants, such as *Stanleya, Xylorrhiza, Oonopsis,* and a number of species of *Astragalus,* grow only on soils high in selenium content. Although these plants seldom poison livestock, their presence is a reliable indicator of the presence of sele-

nium soils. The plants that most commonly cause poisoning are those selenium accumulators that grow just as well as soils lacking selenium. Among the most frequently grazed of these selenium-accumulating plants are various species of *Aster, Atriplex, Castilleja, Sideranthus,* and *Gutierrezia.* Fortunately, most of these plants are not very palatable, and they become even less palatable as their selenium content increases. Selenium also can be concentrated by accumulator plants and returned to the soil upon leaf drop; thus, it is concentrated in the soil around these plants. As a result, relatively palatable, nonaccumulating plants, such as grasses that grow close to the perennial accumulator plants, become toxic.

Concentrations of silica in some grasses is suspected of contributing to urinary calculi (water belly) in cattle and sheep (Ellis 1956). A highly significant correlation has been found between the amount of silica in forage and the incidence of urinary calculi in Montana (Parker 1957).

The only other mineral worth mentioning that is accumulated by plants is molybdenum. Either an excess or a deficiency of this mineral can be toxic. Members of the Leguminosae family can accumulate high levels of molybdenum. Livestock can be poisoned if they continuously graze legumes with a high content of this mineral.

Repellents

Chemical constituents in plants that are simply distasteful to livestock might be viewed somewhat as a mixed curse. On the one hand, they adversely affect palatability; on the other, if it were not for unpalatable plants on unmanaged ranges, there might not be any plants. We do not know precisely why some plants are taken more readily than others. However, we do know that palatability varies with the interrelationship of plant, animal, and environmental conditions.

Organic and inorganic composition, aroma, morphology, succulence, harshness, hairiness, leaf-to-stem ratio, associated species of plants, and even weather conditions can influence how readily an animal will graze a certain plant (Joint Comm. A.S.A. et al. 1962). Some of these are obviously chemical characteristics—organic and inorganic compounds. Since they adversely affect palatability, they might be considered repellents.

For example, a high content of certain essential oils is thought to adversely affect palatability. This is probably at least one of the reasons why *Artemisia tridentata* is not eaten more readily by livestock. Low palatability of *A. tridentata* is unfortunate, for it is one of the most abundant and widespread of our range shrubs, and is recognized as a nutritious winter browse (Smith 1957; Short et al. 1966). However, Cook et al. (1952) suggest that its metabolizable energy is lower than that indicated by its digestible energy values; inaccurate estimates of energy are obtained because of the high content of essential oils. Essential oils are not only responsible for some palatability differences between species, but also for some of the differences in palatability between plants of the same species. Approximately 20 percent more essential oils were found in ungrazed *Juniperus scopulorum* and *J. utahensis* than in nearby grazed foliage of the same species (Smith 1950).

Although lignin is not ordinarily considered a repellent factor, there is some evidence suggesting it might be. Studies with both sheep and cattle have shown that the amount of organic material eaten decreases about 6 percent for each 1-percent increase in lignin content of the forage (Forbes and Garrigus 1950). Lignin also appears to actually decrease the overall digestibility of the constituents that are ordinarily digestible.

No doubt, many other chemical substances act as repellents. Some of these probably render unpalatable otherwise nutritious forage. Others, however, sometimes perform a very useful function. Many poisonous plants are not readily eaten because of the presence of substances animals find objectionable. This presence, of course, minimizes livestock losses on well-managed ranges.

STRUCTURAL FEATURES

Mechanically Damaging Features

Several structural characteristics of range plants are injurious to livestock. These characteristics are in the following categories: Sharp, stiff, or barbed awns and floret bases; spiny fruit or seed coat; barbed or spiny stems; and abundance of hairs or fibers. These features seldom kill, but the affected animals are usually weakened. Secondary effects are often more severe than the direct injury. For example, puncturing of the skin of animals by plants with sharp floret bases, awns, or spines allows entrance of screwworms and fungi (Stoddart and Smith 1955). Most troublesome, perhaps, is entrance of the fungi that causes actinomycosis, or lumpy jaw.

Certain grasses, particularly on our dry western ranges, possess both sharp floret bases and awns. These include various species of *Stipa* and *Aristida* (Durrell et al. 1950; USDA Forest Service 1937), as well as *Bromus rigidus* and *Avena fatua* (Stoddart and Smith 1955). After the plants mature, the awns and florets penetrate the soft skin of parts of the animal's mouth and eyes, causing irritation. The barbed bristles at the base of the florets of *Setaria lutescens* easily penetrate the skin and

flesh, and are kept there by the barbs (Kingsbury 1964). The long, barbed awns of *Hordeum jubatum* make it one of the worst plants for causing mechanical injury to the eyes and mouth of range livestock as well as of elk, deer, and antelope (USDA Forest Service 1937). Occasionally, the awns of the ubiquitous *Bromus tectorum* work into the tongue and soft mouth tissue to cause inflammation (Durrell et al. 1950).

The spiny covering around the seeds of *Cenchrus pauciflorus* has caused hoof irritation (Durrell et al. 1950), and the spiny fruits of *Tribulus terrestris* can cause external and internal injuries if inadvertently fed in hay (Muenscher 1947).

The stiff spines and barbs on the stems of certain range plants are at least potentially injurious to livestock. Such plants include *Opuntia* spp. (Muenscher 1947) and *Rubus macropetalus* (Kingsbury 1964). The latter species is considered good browse for stock in western Washington and Oregon (U.S. Forest Service 1937), but the thorny stems occasionally become lodged in the nasal passages of cattle (Kingsbury 1964).

A few range plants have fibrous or hairy characteristics that sometimes cause trouble when eaten. *Verbascum thapsus* and *Eremocarpus setigerus*, for example, are covered with dense mats of hair that can form solid, indigestible balls in the digestive tract, particularly of sheep (Muenscher 1947). The fibers in *Yucca* spp. occasionally cause the same problem (Stoddart and Smith 1955).

Deterrents

Whereas some structural features actually injure grazing animals, others merely discourage use. Various species of *Opunita* are usually avoided because of their numerous sharp spines. When these are removed, the fleshy stems are readily eaten by both sheep and cattle (U.S. Forest Serv. 1937). On large areas, such species as *Opuntia arborescens* also form a barrier to the use of palatable forage growing with it. Spines and barbs of other range plants no doubt serve equally as barriers to livestock grazing.

The overall coarseness of plants and a high proportion of stems to leaves are two more structural deterrents to use that might be considered. If given the opportunity, grazing animals are highly selective of what they eat. Rank, harsh vegetation, as well as that with a high crude fiber content, is generally avoided (Stoddart and Smith 1955; Joint Committee A.S.A. et al. 1962). Sheep are known to prefer leaves over stems (Cook et al. 1948). Grasses that tend to retain dry flower stalks from the previous growing season are preferred less than those that do not. Livestock will avoid this coarse, dry material as long as other more desirable forage is available.

PHYSIOLOGICAL ATTRIBUTES

A number of physiological attributes of plants are considered undesirable from the standpoint of range management. These are not usually considered as being in the same realm as poisonous or physically damaging properties. Their influence is more indirect and more subtle. However, the value of range plants for forage production is greatly affected by their physiological characteristics.

As an example, much of our western range is subject to summer drought so intense that many of the species become dormant and dry. The inability of a species to become summer-dormant may decrease its resistance to damage from grazing. *Stipa comata*, which does not become dormant during the hot summer months in southern Idaho, is more susceptible to herbage removal in the summer than is *Sitanion hystrix*, which does become dormant (Wright 1967). Regrowth in late summer and fall following summer dormancy depends not only upon rainfall but upon the plant's ability to break dormancy and to produce new leaves. Species physiologically unable to do this are probably less desirable on such ranges than those that do have substantial regrowth. In this regard, perennial grasses appear superior to forbs.

Changes in nutrient content of herbage during the growing season and during dormancy are important considerations in evaluating range species. Nutrient content generally decreases as the growing season advances and plants mature. Some range grasses in North Dakota lose more than 70 percent of their protein by the end of summer (Whitman et al. 1951). However, the amount of decrease is at least partly an inherent characteristic that varies among species. At a time when other prairiegrasses become very low in protein, the protein content of *Bouteloua gracilis* has been known to increase (Williams 1953). Usually the nutrient decrease is most pronounced in forbs and is least noticeable in shrubs. Although the nutrient content of shrubs is generally less than that of grasses and forbs early in the growing season, by fall the reverse is true —especially with regard to protein level because of the differences in rate of loss (Blaisdell et al. 1952; Oelberg 1956). Seasonal changes of nutrient content in shrubs are greater in deciduous species than in evergreen species (Short et al. 1966).

Nutrient content, then, varies not only between species, but species differ in their ability to retain nutrients. Physiological characteristics that cause plants to rapidly lose nutrients are undesirable. Attributes that permit plants

to retain high nutrient levels to maturity and, even better, through dormancy, are preferred.

Numerous other plant characteristics have a direct effect on the value of a range plant for forage production. Included would be features affecting establishment and growth, persistence, and production efficiency. Annuals are usually less desirable than perennials because of greater yearly fluctuations of forage production. Rhizomatous species are usually superior to nonrhizomatous species because of greater flexibility in methods for establishment and survival. Physiological and morphological attributes contributing to grazing, drought and freezing resistance are of major importance.

Available moisture is the major limitation to forage production on many of our western ranges. A high water consumption to forage production ratio for a species is a decidedly objectionable characteristic, particularly for a plant growing on arid rangeland.

OTHER CONSIDERATIONS

Most poisonous plants are eaten in harmful quantities only when livestock are forced to do so (U.S.D.A., A.D. & P.R.D. 1964; Durrell et al. 1950; Stoddart et al. 1949). Certain species of *Prunus, Delphinium, Lupinus, Triglochin,* and *Astragalus* may be exceptions (Stoddard et al. 1949). Livestock are forced to eat poisonous plants because of poor management. Poor management has numerous forms, but the most obvious is extreme overgrazing where the livestock are left little but poisonous species to eat. Placing livestock on a range before substantial growth of good forage has occurred and where early-growing poisonous plants are abundant is another form of poor management. It is definitely poor management to rapidly drive hungry animals through areas containing poisonous species. In all these cases, livestock are not given the opportunity to be selective. Consequently, they eat almost anything to satisfy their hunger.

Many livestock die because they are trailed across ranges infested with poisonous plants. Such losses can generally be reduced substantially by feeding them supplements before placing them on such ranges. Repeated feeding of specific supplements has effectively alleviated poisoning by certain species. Oxalate poisoning by *Halogeton* and *Sarcobatus* usually can be prevented if sheep are fed a daily grain or alfalfa pellet supplement containing 10-percent dicalcium phosphate (U.S.D.A., A.D. & P.R.D. 1964). The use of salt containing sulfur in a 12:1 ratio or the addition of about 1-percent maltose or glucose sugar to the daily ration (Durrell et al. 1950) has been reported helpful in lessening prussic acid poisoning in animals of the cyanogenic species. Poisoning from the glycosides in *Helenium hoopesii* can be reduced by daily feedings of a mineral-oil supplement containing seven parts trace-mineralized salt and three parts dicalcium phosphate (U.S.D.A., A.D. & P.R.D. 1964). Development of such alleviants is a promising approach to the problem of learning how to safely use the forage produced on ranges where poisonous plants are found.

Poisonous plants seldom grow in such abundance as to justify extensive eradication programs. Judicious management will usually prevent livestock losses. For this reason, the potential problem caused by the presence of poisonous plants should be carefully considered in any proposed grazing system. Both choice of season and choice of animal come into play. For example, it would be foolhardy to intensively graze a lupine-infested range in late summer with sheep, even though this same range might be intensively grazed in early summer without danger. Similarly, use of larkspur-infested ranges could be fatal to cattle, but these might be safely grazed by sheep. In all cases, grazing influences should be controlled so that they do not promote an increase in the toxic species. Such considerations must be carefully evaluated and incorporated into management systems designed for specific range areas.

The problem of nutritious but unpalatable species is even more challenging. Just why do animals refuse to eat many of our abundant range plants? Some investigators maintain that the grazing animal instinctively selects the most nutritious species (Stapledon 1947; Ellison 1948). Others disagree with this hypothesis (Tribe and Gordon 1950). Smell, taste, and touch have been shown to markedly affect forage preference (Arnold 1966b); however, sight apparently is insignificant (Arnold 1966a). Plice (1952) found that cows have a definite "sweet tooth" and readily graze usually unpalatable forage sprayed with sugar solutions or even with noncaloric artificial sweeteners. Palatability and utilization of rank, dry forage can be greatly increased in some cases by spraying with molasses (Wagnon and Goss 1961). Fertilizing with available phosphorus has been suggested as a means to increase the sugar content of forage and thus enhance palatability (Plice 1952). If we better understood the chemical constituents contributing to the unpalatability of certain species, we would be better able to develop techniques to nullify their objectionable effects.

Our knowledge of the forage values of range species is still fairly superficial. Our judgments are largely based upon what the cow likes. This could be equated to feeding one's children a diet of cookies, cake, and candy—that is what they like! A critical evaluation of a species' value for producing range forage should

include, among other factors, nutritive content, productive efficiency, resistance to grazing and climatic extremes and the objectionable characteristics already discussed. Of course, the plant must be sufficiently palatable so that livestock will eat it in quantity. When we know which species to favor, techniques must be developed to shift vegetation composition toward an abundance of these selected species. Once this is done, we will begin to achieve the full productive potential of our rangelands.

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Supplementing Range Forage

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Supplementing the range diet in order to better meet the nutritional requirements of livestock is one approach to more effective use of available range forage. Theoretically, determining supplemental needs should involve straightforward calculation of balanced diets based on composition of the forage and on nutrient standards developed by the Committee on Animal Nutrition of the National Academy of Sciences-National Research Council (193, 1964) by Morrison (1954) and others. However, on rangelands, the approach is complicated by extremely heterogeneous and variable forages, and is limited by a lack of nutritional information, including digestibility of range forages.

Supplementation varies considerably in the United States in relation to regional climate and the associated differences in forage quality and livestock management. In the semiarid West, range soils generally are capable of supporting plants that provide high-quality forage during the growing season. Deficiencies may occur as forage matures, and these can be important to growing animals. The clearest need for supplemental feeding in the West is on dormant, winter range. Substitute feeds required during emergencies, such as snowstorms and severe droughts, will not be considered as supplements in this discussion.

The situation is quite different on pineland ranges of the humid South (including the Southeast, as used in this paper) where relatively infertile soils produce forage of limited quality. Nutritional levels vary seasonally, but deficiencies prevail most of the year. Supplementation and other practical means of providing an adequate, yearlong diet for livestock are especially needed to effectively utilize range resources.

This paper discusses several aspects of supplementing range forage to meet the nutritional levels required for commercial livestock production. Economic aspects (i.e., costs vs. returns) are not treated directly, but supplementation questions are considered essentially economic.

PRACTICAL CONSIDERATIONS

Range grazing is generally an extensive livestock operation based on low-cost feed; supplemental feeding on range is essentially an economic question to be decided by balancing costs against additional production (Stoddart and Smith 1955; Cook and Harris 1968). Although range diets may not be optimum, supplemental feeding has been economical only in special circumstances which involve minor portions of the total animal diet. Aside from emergency periods requiring substitute feeds, these special circumstances include protein and mineral imbalances that prevent animals from effectively using digestible nutrients.

Type of Operation

Throughout the United States, livestock operations have been adapted to the quality of available range resources in order to reduce needs for expensive supplementation. Producing grass-fat beef or lambs requires a ration containing about 8 percent digestible protein and 65 percent total digestible nutrients (TDN); yearling cattle make normal growth on 5 to 7 percent digestible protein and about 50 percent TDN; cows nursing calves need about 5 percent digestible protein and 60 percent TDN; mature, pregnant cows need 4.5 percent digestible protein and 50 percent TDN (NAS–NRC 1963). Thus, a cow-calf operation, in which calves are sold when weaned at the end of the best grazing period, has been considered the most practical period for utilizing range of limited quality much of the time, because mature, nonlactating animals subsist on low-quality range better than do growing animals with higher nutritional requirements. Southern ranges are used almost entirely in cow-calf operations. In the West, practical alternatives include production of stocker and feeder or even grass-fat livestock, depending largely on the nutritional level of available range forage. Alternatives might be increased with development of new supplemental feeding methods, but other approaches to coping with limited forage quality continue to warrant consideration.

Minimizing Supplement Needs

Where possible, adjusting the grazing period to coincide with the growth period of main forage plants optimizes diet quality and minimizes need for supplementation. In the mountainous West, shifting livestock seasonally to ranges having different growth periods associated with elevation results in optimum use of forage. In other regions, some opportunities exist for beneficial adjustment of grazing season among range types, such as between tobosa

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grass ranges during the growing season and black grama ranges in the dormant season in the Southwest (Paulsen and Ares 1962). A mixture of browse and grass range is desirable in the West during the dormant season when good browse has adequate protein and grass has adequate energy (Cook and Harris 1968). Where appropriate, seasonal range types do not exist naturally; they often can be established through seeding or other management practices.

Range improvement practices offer promising alternatives to supplementation, especially when they also increase forage yield. It is well known that seasonal forage quality often can be increased, or the period of adequate quality extended, by altering the botanical and chemical composition through range seeding, fertilization, burning, mechanical or chemical treatments, and grazing management. In western range seeding, extension of adequate forage quality has long been a major consideration in selecting species to be seeded. In some situations, profitable fertilization can correct phosphorus deficiency and replace supplementation, as in southern Texas (Reynolds et al. 1953). Prescribed burning improves forage quality and cattle gains in the southern pine region, but its effects are short-lived. Also, it does not eliminate deficiencies nor the need for supplementation in this region (Halls et al. 1952; Campbell et al. 1954).

Early weaning of calves can reduce the need for supplementation on ranges when forage quality drops below adequate levels during late summer; this frequently occurs in dry years in the West (Skovlin 1967). Because requirements for protein and digestible nutrients of lactating beef cows are more than 50 percent greater than for dry cows, and because about 2.5 pounds of TDN are required to produce 1 pound of TDN in milk form through the cow, it is more efficient to feed calves directly than through the dams. Calves weaned at about 4 months of age have gained as well as calves weaned when they are 6 months older (Frischknecht 1968). Following early weaning, dry dams tend to gain in condition and were reported to graze farther into rough range than when they had calves at their sides.[2]

Practical Levels

Short periods of deficient diet are not serious if followed by high-quality diets. In Montana and California, breeding herds that were allowed to lose 150 to 200 pounds during the winter calving season, but were gaining weight and condition rapidly during the following breeding season, produced calf crops approaching 90 percent (Reed and Peterson 1961; Wagnon et al. 1959). Sheep in the West successfully tolerate deficient diets and weight loss on winter range when they make rapid gains on spring range; supplementing at levels that fully maintain weight in winter is not considered economical (Harris 1968).

However, where the range diet does not permit lactating cows to gain weight and to breed successfully, as in the Southeast, alternate-year calving and 50-percent calf crops tend to be the rule (Shepherd et al. 1953; Southwell and Halls 1955). Thus, for breeding herds, the percentage of calf crop can reflect major supplement needs. In the South, supplementation involves more than the wintering period (Duvall and Whitaker 1963; Southwell and Hughes 1967).

Apparently young animals also can be wintered successfully at nutritional levels that scarcely maintain weight if the subsequent diet is of a high quality. Studies have shown that young beef cattle can recover from severe undernutrition (one-sixth of the protein and two-fifths of the energy allowances for rapid growth) lasting as long as 6 months without impairing subsequent growth or quality when finished on a liberal diet, and without reducing their overall efficiency of feed utilization (total feed per pound of gain) (Winchester et al. 1967; Winchester and Ellis 1957). This work verifies the common observation that animals show greater efficiency in feed utilization and gain faster after undernutrition. It also supports the common practice of providing only enough supplement on winter range to prevent serious loss in livestock condition (Harris 1968; Morrison 1954).

DEFICIENCIES AND SUPPLEMENTATION

The most commonly recognized deficiencies in range forage for livestock are energy, protein, phosphorus, and carotene (vitamin A). Customary salting practices usually satisfy requirements for sodium and chlorine. In the South, deficiencies also occur in calcium and several minor elements, including iron, copper, and cobalt (Cunha et al. 1964). Iodine deficiency occurs in several Western states (Stoddart and Smith 1955).

Supplement requirements can be estimated from NAS–NRC nutritional standards developed by its Committee on Animal Nutrition (NAS–NRC 1963, 1964). However, confident estimating requires specific information about the digestibility and the chemical composition of the range diet. Such information is scarce, but some inferences can be drawn from available data on chemical composition by assuming levels of digestibility. As a guide to judging forage adequacy, table 1 summarizes livestock

[2] McArthur, J. A. B. Personal correspondence, Oreg. State Univ., Eastern Oreg. Exp. Sta., Union, Oreg., 1968.

TABLE 1.—*Required content of major nutrients in the feed*[1] *of selected classes of cattle and sheep* (NAS–NRC 1963, 1964)

Class, size, and rate of gain	Protein	DP[2]	DE[3]	TDN[3]	Ca	P
	Percent		*Kcal./lb.*	*Percent*		
Beef Cattle						
Steers and heifers, normal growth:						
400 lb.; 1.6 lb./day	11.7	7.0	1,050	53	0.29	0.21
800 lb.; 1.2 lb./day	7.8	4.7	1,000	50	.18	.15
Wintering weanling calves:						
400 lb.; 1.0 lb./day	10.3	6.2	1,000	50	.27	.21
600 lb.; 1.0 lb./day	9.1	5.5	1,000	50	.20	.16
Wintering yearling cattle, 800 lb.; .7 lb./day	7.5	4.5	1,000	50	.18	.17
Wintering pregnant heifers, 900 lb.; .8 lb./day	7.5	4.5	1,000	50	.16	.15
Wintering mature pregnant cows:						
800 lb.; 1.5 lb./day	7.5	4.5	1,000	50	.16	.15
1,000 lb.; .4 lb./day	7.5	4.5	1,000	50	.16	.15
1,200 lb.; −.5 lb./day	7.5	4.5	850	43	.16	.15
Cows nursing calves, first 4 mos. 900–1,100; .0 lb./day	8.3	5.0	1,200	60	.24	.18
Sheep						
Nonlactating, first 15 weeks of gestation:						
120 lb.; .07 lb./day	8.0	4.4	1,000	50	.24	.19
160 lb.; .07 lb./day	8.0	4.4	1,000	50	.20	.16
Last 6 weeks of gestation:						
120 lb.; .37 lb./day	8.4	4.6	1,040	52	.24	.18
160 lb.; .37 lb./day	7.8	4.3	1,040	52	.22	.16
First 9 weeks of lactation						
100 lb.; −.08 lb./day	8.7	4.8	1,180	59	.30	.22
160 lb.; −.08 lb./day	8.0	4.4	1,100	55	.27	.20
Replacement lambs and yearlings:						
80 lb.; .20 lb./day	8.7	4.8	1,000	50	.20	.18
120 lb.; .07 lb./day	7.0	3.9	1,000	50	.20	.18
Fattening lambs, 70 lb.; .40 lb./day	11.0	6.1	1,160	58	.21	.18

[1] Based upon air-dry feed containing 90 percent dry matter.
[2] Digestible protein: total protein assumed 60 percent digestible for cattle and 55 percent for sheep.
[3] One pound total digestible nutrients (TDN) assumed equivalent to 2,000 kcal. of digestible energy (DE).

requirements in percentages of digestible nutrients in the diet. These have been calculated by NAS–NRC from daily nutrient requirements and assumed levels of feed intake and digestibility. Their alternative standards for daily requirements of nutrient weight are appropriate for computing supplemental rations.

Energy

Supplementing range with energy feeds seems rarely justified. Although lack of energy is considered the most common manifestation of nutritional deficiency of livestock (NAS–NRC 1963, 1964), this can result from limitations in either the amount or the quality of feed. From the viewpoint of supplementation, we are concerned primarily with forage quality because it can be assumed that quantity can best be provided through grazing management.

Energy feeds might be considered as substitutes rather than supplements for range forage because energy is the major component of the animal diet. However, the practice of providing energy feeds to carry livestock through emergency periods permits practical utilization of range during otherwise hazardous seasons. Appropriate levels of emergency supplements are shown in standards for wintering livestock (Morrison 1954, NAS–NRC 1963, 1964). For example, the daily energy requirements for maintaining weight of a pregnant, 1,000-pound cow could be met by the equivalent of 11 pounds of corn or 17 pounds of good alfalfa hay daily. Pelleted commercial feeds will likely be fed on range where hay is not readily accessible. A common practice is to feed individuals or lots of animals as necessary to keep them in fair condition.

Western range forage generally does not seem critically deficient in energy; however, specific information is scarce. Even during winter, when forage values are lowest, Western grassland ranges seem to maintain livestock adequately with only protein supplement (Smith et al. 1967). Grasses of Western semi-

desert and salt desert ranges usually furnish adequate energy in the dormant stage (Bohman et al. 1961; Cook and Harris 1968) Cheatgrass (Cook and Harris 1952) and California annual range (Van Dyne 1965) also furnishes enough energy, except after extensive leaching by winter rain (Wagnon et al. 1959). Dormant browse plants tend to be deficient in energy, but these are good sources of protein and carotene (Cook and Harris 1968). A high-energy supplement is recommended for wintering sheep on sagebrush range, and as a substitute feed during deep snow emergencies (Harris 1968). Energy values of range forage and animal diets vary markedly with species, range condition, degree of use, and other factors which can be influenced through management. Skillful handling of these factors is generally the most practical approach to meeting energy requirements of livestock on Western ranges.

In the South, however, digestible energy appears to be the main limitation of range forage. On bluestem forest range in Louisiana, estimates from composite samples representing cattle diet indicated adequate energy only during the young-leaf stage. Indications were that a 700-pound lactating cow would need 1 to 1.8 pounds of supplemental TDN per day during the full-leaf and mature-green stages, and about 3 pounds on winter rough (Campbell et al. 1954). However, feeding small amounts of energy supplement (in addition to protein and minerals) during winter was not profitable (Duvall and Whitaker 1963).

On wiregrass forest range in Georgia, digestion trials with indicator techniques showed TDN at only 44 to 48 percent in April and June, 42 to 48 percent in September, and 32 to 33 percent in December (Halls et al. 1957; Hale et al. 1962). In the spring and summer, these levels approximate requirements for maintenance of mature cattle without weight gains (as recommended for economic wintering), but they fall far short of the standards for nursing cows—60 percent TDN (table 1). This explains why cows lose weight while suckling calves and tend to have small calf crops when this kind of range is supplemented with only protein and minerals (Halls and Southwell 1956; Shepherd et al. 1953). Integration of improved pasture with wiregrass range in summer, to provide about half the diet, offers one economical method of providing adequate energy levels to obtain good calf crops (80 percent) and weaning weights (400–450 pounds) from low-quality wiregrass range (Southwell and Hughes 1965).

Protein

Protein supplementation is often a practical means of improving livestock production and effective utilization of range forage, especially in fall and winter when mature grass is deficient in protein. Although vital to animal health, vigor, growth, and reproductive efficiency, digestible protein only need comprise a relatively small proportion of the diet—4 to 5 percent for most classes of sheep and cattle except rapidly growing young animals (table 1). Also, supplying deficient protein may increase the digestibility of other nutrients (Harris 1968).

Common protein concentrate meal feeds for cattle and sheep—cottonseed, soybean, meal, and peanut meal—usually have 41 to 45 percent total protein, and 33 to 43 percent digestible protein. Consequently, relatively small amounts will satisfy the daily requirement of common classes of range livestock (NAS–NRC 1963, 1964):

Class of livestock	*Digestible protein*	*43 percent digestible protein*
	(Lb./animal daily requirement)	
Normal growth, young cattle (400–800 lb.)	0.9	2.1
Wintering weanling calves (500–600 lb.)	.8	1.8
Wintering yearling cattle (600–900 lb.)	.7	1.6
Wintering pregnant cows (900–1,200 lb.)	.8	1.8
Cows nursing young calves (900–1,100 lb.)	1.4	3.2
Ewes (120 lb.) last 6 weeks gestation	.19	.4
Ewes (120 lb.) early lactation	.23	.5
Replacement lambs and yearlings (80 lb.)	.15	.3
Fattening lambs (80–100 lb.)	.20	.5

Urea and some other nonprotein nitrogen compounds, including diammonium phosphate, can replace part of the costlier protein in livestock feeds, but their use as range supplements has not been thoroughly investigated. Rumen bacteria can convert urea and other nitrogenous compounds into proteins for the animal. About one-third of the total protein requirement may be met in this way under suitable conditions (NAS–NRC 1963), including ample, readily available carbohydrates, phosphorus, trace minerals, and sulfur. Fifty-percent replacement of protein with urea and with diammonium phosphate has been successful in fattening steers (Brown et al. 1967; Gallup et al. 1953). Pelleted protein supplement with 25 percent of its nitrogen as urea was as good as cottonseed meal for supplementing winter range in Oklahoma (Gallup et al. 1953). Biuret, a new source of nonprotein nitrogen, may be better than urea as a protein substitute (Raleigh and Turner 1968).

In general, protein supplementation is profitable when it increases the reproductive rate

of breeding herds, reduces death losses, and permits replacement of costlier sources of feed or forage on the range—especially in winter. It makes grass range throughout the West suitable for wintering young animals as well as mature breeding stock (Harris 1968; Marion et al. 1956; Pope et al. 1956; Smith et al. 1967). Where browse comprises much of the diet, protein supplement is less advantageous because desirable browse species usually contain adequate protein (Cook and Harris 1968).

On California annual range, protein supplementation during the mature-forage stage has been found economical for weaner calves, yearling cattle, and brood cows. Calves gained an extra half-pound per pound of cottonseed cake, and retained 75 percent of this advantage through the subsequent green grazing period; breeding cows produced a higher calving percentage (83 vs. 66) and heavier calves, and returned 0.4 pound of weaned calf per pound of supplemental feed (Wagnon et al. 1959).

Elsewhere, protein supplementation sometimes extends gains of calves or yearlings on maturing spring or summer range, such as crested wheatgrass in the Northwest, but not necessarily at a profit (Wallace et al. 1963). On such range in Utah, protein supplement during summer and fall increased gains of lactating cows, but not of calves or yearlings (Harris et al. 1968). Obviously, increased weight must be marketed if supplementation is to be profitable. A weight advantage on young animals can disappear during the following season of high-quality forage, when thin animals tend to gain fastest (Morrison 1954).

Southern ranges are deficient in digestible protein much of the year (Campbell et al. 1954; Halls et al. 1957), but response to protein supplementation appears restricted somewhat by limited digestible energy. On bluestem range in Louisiana, protein supplement from October to May (plus limited hay in late winter and minerals year around, produced profitable calf crops (80 percent) and weaning weights (433 pounds) (Duvall and Whitaker 1963). However, supplementing only from November through March seems as effective and more profitable (Duvall and Hansard 1967).

On wiregrass ranges in Georgia, supplementation with protein concentrate has not been as effective as with improved pasture which provides more energy (Southwell and Hughes 1965). For example, range plus 0.6 acre of improved pasture in spring and summer produced about 90 more pounds of weaned calf per cow than did range plus 1 to 2 pounds of protein meal per cow daily. Digestible energy of native wiregrass forage in late winter was considered too low for economic utilization; cattle were wintered on hay and field gleanings.

The equivalent of 1 to 2 pounds per day of cottonseed or soybean meal per cow and one-fourth to one-third pound per sheep are customary rations that have been profitable. Higher rates are often fed as a convenient, but expensive, energy supplement.

To save labor, protein supplements may be fed two or three times weekly; results are similar to those obtained with daily feeding (Harris 1968; Melton et al. 1961). Also, protein supplement can be self-fed safely by using salt, or salt and mineral mixed, to control intake (Cunha et al. 1964; Harris 1968; NAS–NRC 1963). As much as 2 pounds of salt per day is not toxic to cattle if they have ample drinking water.

In mixtures of 20 to 25 percent salt with cottonseed meal, yearling cattle have consumed from about one-half pound of salt daily in the Southwest (Ares 1953) to approximately three-fourths pound in Oklahoma (Nelson et al. 1954). These rates of salt maintained protein-meal intake at desired levels of 1.5 to 2 pounds daily. The recommended procedure is to start with a mixture of 20 to 25 percent salt with the protein supplement, and then to reduce the salt content to increase total consumption, or vice versa. Where a mineral mixture is also being fed, the desired amount should replace an appropriate portion of the salt (Cunha et al. 1964).

Minerals

Sodium and chlorine requirements of range livestock are satisfied by the usual practice of feeding loose salt, rock salt, or block salt free choice on range. Young, growing cattle and mature sheep need 10 to 12 grams of salt per day, or about 0.8 pound per month; and lactating cows, about 1.8 pound per month (NAS–NRC 1963, 1964). Free-choice consumption varies widely with season and location, but 20 pounds per cow is commonly used in planning annual requirements in the West (Morrison 1954; Stoddart and Smith 1955). On experimental ranges in Louisiana, Georgia, and Florida, cattle have consummed 23 to 36 pounds annually in mixtures with phosphorus sources and other minerals (Cunha et al. 1964; Duvall and Whitaker 1963; Halls and Southwell 1954).

Phosphorus is the major mineral deficiency of range forage (NAS–NRC 1963). *Calcium*, on the other hand, is rarely deficient, except in the Southeast. Phosphorus and calcium occur together in the principal sources of phosphorus supplements—steamed bone meal, defluorinated rock phosphate, and calcium phosphate —so providing adequate phosphorus with these sources will take care of calcium deficiencies.

Supplementation is needed for young cattle and lactating sheep when range forage contains less than 0.20 percent phosphorus, and

for other classes of cattle and sheep when it falls below 0.15 to 0.18 percent (NAS–NRC 1963 and 1964). A deficiency results in lowered appetites, a reduced rate of gain and milk production, and reduced efficiency of feed utilization—particularly of protein. Phosphorus deficiency is common in mature grass forage on western ranges (Morrison 1954; NAS–NRC 1963) and is nearly universal on southern and southeastern ranges (Duncan and Epps 1958; Halls et al. 1957).

Considering the possible benefits and low cost, supplementation appears justified when phosphorus deficiency is likely or suspected. This will include supplementation in fall and winter on most western ranges, and yearround on southern ranges. Total requirements are only 10 to 15 grams per day (0.7 to 1.0 pound per month) for range cattle, and 3 to 4 grams per day (0.2 to 0.3 pound per month) for sheep; lactating animals require about twice these amounts.

Common sources, and their phosphorus content, are: Steamed bonemeal (8–18 percent), defluorinated rock phosphate (9–21 percent), dicalcium phosphate (18 percent), diammonium phosphate (23 percent), and sodium phosphate (12 and 22 percent). The last source is completely soluble and can be added to drinking water.

Although livestock tend to satisfy their phosphorus requirements when bonemeal or other phosphorus sources are offered free choice, salt is commonly added as about one-third of the mineral mixture. To assure adequate consumption in the Southeast, molasses (4 to 8 percent) and cottonseed meal (4 to 6 percent) are added along with salt (30 to 35 percent) to the phosphorus source (50 to 60 percent) and minor elements (Cunha et al. 1964; Hughes and Southwell 1963).

Minor Elements

Iodine deficiency areas occur locally throughout the Northwest, the Dakotas, Montana, Colorado, Utah, Nevada, and Idaho (NAS–NRC 1964). In these areas iodized salt (0.01 percent potassium iodine) is recommended to avoid possible losses in lamb and calf crops.

Other important minor element deficiencies for range livestock are limited to the South Atlantic and Gulf Coast areas, principally Florida (Halls et al. 1964). Iron, copper, and cobalt are included in recommended mineral mixtures as standard practice in Florida, and are often included on other southern ranges. To supply these elements, a typical mineral mixture for beef cattle in Florida will contain about 3 percent red oxide of iron, 0.6 percent copper sulfate, and 0.1 percent cobalt carbonate; most of the mixture is a phosphate source and salt (Cunha et al. 1964).

RESEARCH NEEDED

Supplementation of range diets will become more effective and profitable as knowledge of range nutrition is accumulated. Some of the important research challenges in range nutrition are outlined by Harris (1968). Besides development of better techniques for studying nutrition on the range, and for measuring the nutritive status of range animals, there are challenging possibilities for improving utilization of range forage. With better understanding of the symbiotic relations between rumen microorganisms and the host animal, it may be possible to create an environment in the rumen that would permit more complete or rapid utilization of the polysaccharide energy in range forage, and to convert some of the indigestible fiber into animal tissue and milk. New nitrogen supplements are needed to replace expensive protein feeds, such as soybean meal, and also to provide a sustained supply to rumen microorganisms under range conditions where it is impractical to supplement frequently. This would permit long-term supplementation with a minimum of livestock handling and cost. An example is the use of sustained-release pellets to supply cobalt in Australia.

One new source of nonprotein nitrogen that shows promise is biuret, a condensation product of urea. It releases nitrogen in the rumen more slowly, and is less toxic and more palatable to livestock than urea. It was more effective and more profitable than urea and cottonseed meal for summerlong supplementation of crested wheatgrass range in Oregon (Raleigh and Turner 1968).

SUMMARY

Specific needs for supplementing range forage are not clear because information on digestible nutrients in the heterogeneous and variable range forages is scarce. Only general inferences can be drawn from fragmentary data and indirect evidence. Deficiencies are most obvious on pineland ranges of the South (including the Southeast).

Under characteristic range livestock operations, supplemental feeding is not always the most profitable approach to overcoming deficiencies in range diets. Besides adapting the livestock operation to the kind of range available, alternatives for providing adequate diets and minimizing supplementation include: (1) Grazing available range types at optimum seasons, and at rates that provide ample quantities of forage; (2) improving the botanical and chemical composition by range seeding, burn-

ing, chemical, or mechanical treatments, and by other range improvement practices; and (3) early weaning of calves when forage quality drops below requirements of lactating cows.

Short periods of deficient diet and weight loss and then periods of high-quality diet usually do not decrease livestock productivity and efficiency. Accordingly, supplemental feeding in the West appears practical primarily on dormant winter range and only at levels that prevent serious loss in livestock condition. In the South, however, supplementation of native range is also necessary in other seasons.

Common deficiencies in range forage are energy, protein, phosphorus, iodine, and carotene. Deficiencies in calcium and several minor elements also occur in the South. Customary salting practices usually satisfy animal needs for sodium and chlorine.

Energy deficiency seems nominal on western range, but it evidently is a limiting factor of southern forest ranges. Supplementing range with energy feeds appears impractical except for limited periods of emergency.

Protein deficiency can be expected on most grassland range during the dormant season. Protein supplementation is profitable on many winter ranges in the West, and is practically essential on southern ranges.

Phosphorus supplementation, particularly when forage is mature, is desirable on many western ranges; it is always needed on southern ranges, along with calcium in most cases.

Other deficiencies are relatively restricted: Iodine in widespread but localized western areas; iron, copper, and cobalt in part of the South; and carotene where green forage is lacking for several consecutive months.

Range supplementation will become more profitable as knowledge of range nutrition is accumulated through research. In addition to better techniques, range nutritionists need better understanding of rumen microorganisms and possibilities for creating a rumen environment conducive to better utilization of range forage. Also, they should investigate new nitrogen supplements that will be economical and also provide a sustained supply to rumen microorganisms under range conditions where frequent feeding is impractical.

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DETERMINING FORAGE QUALITY

Digestibility Trials: *In Vivo* Techniques

HENRY L. SHORT[1]

The way the nutrient composition of food changes during animal digestion is a good indicator of forage value and range quality. The measurement of these changes and the evaluation of their meaning are discussed in this paper. Factors affecting the digestibility of forage, such as plant species phenological stage, and forage nutrient quality, are not considered.

Macro- and microdigestion techniques are covered separately. Macrodigestion data are obtained from standard digestion trials with animals confined in a dry lot, barn, or range. In *in vivo* microdigestion studies forage samples are suspended within the digestive tract of experimental animals, and changes in the nutrient composition of these samples are measured.

SOURCES OF ANIMAL VARIATION

Anatomical and physiological differences in the digestive systems of animal species are responsible for large variations in ability to digest foodstuffs. The storage and fermentative organs in digestive tracts of many animals are discussed by Moir (1965). Stomach capacity is about 60–70 percent of the total digestive capacity of cats, dogs, sheep, goats, and cows (Dukes 1955). The digestive tract of herbivores, in both absolute terms and in relation to body volume, is many times larger than that of carnivores. Ruminants have a very large stomach; other herbivores, such as the pig and horse, have capacious small intestines and colons.

Animals with such diverse digestive systems as the rat, guinea pig, sheep, pig, and man have similar ability to digest foods with low fiber content. However, as diets become increasingly fibrous, ruminants, with their voluminous digestive tracts and symbiont microbial populations, have major digestive advantages.

Differences in digestive ability between breeds of cattle, between cattle and sheep, and between other ruminant species are reviewed by Hungate (1966). Because of their larger rumen reticulums, cattle probably digest fibrous forage more thoroughly than do deer of the genus *Odoceilus* (Short 1963). Roe deer (*Capreolus capreolus*) apparently are less able to digest fibrous forages than are the larger red deer (*Cervus elaphus*) (Brüggemann et al. 1965).

Although suitable domestic analogues can sometimes be found for particular wild species, data that are extrapolated to little-studied herbivores are always suspect. The additional expense of dealing with the wild herbivore can probably often be justified.

MEASUREMENTS OF FORAGE UTILIZATION

The first approximation of animal use is digestible energy or total digestible nutrients (T.D.N.). Digestible energy is the gross energy of the foodstuff minus the gross energy of the feces. If bomb calorimetric data are not available, the apparent digestibility of forage components can be arithmetically equated to T.D.N. In most digestion trials with wild herbivores, digestible energy has been measured.

Metabolizable energy is the difference between the gross energy of a feed and the gross energy of feces, urine, and gases of fermentation from the gastrointestinal tract. Urine is collected with a harness and collection bag or with a gravity delivery system in a metabolism cage or respiration chamber. Gas from fermentation processes is collected and measured either in respiration chambers or with face masks and spirometers. An advantage in measuring metabolic energy in forest and range animals is that some important forages contain volatile substances that are excreted mostly in the urine. Measuring apparent digestible energy of these forages overestimates their usefulness to herbivores. Ruminants frequently lose about 10 percent of digestible energy in

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urine and 8 percent as gases of fermentation (Byerly 1967).

Net energy is the most refined measure of the usefulness of food for herbivores. It is the energy remaining after metabolic energy (fecal and urinary and combustible gases of fermentation) and heat losses due to nutrient utilization have been deducted from the gross energy of a feed. The net energy of energy balance studies is that available for maintenance, work, or secondary production (pregnancy, lactation, etc).

Digestion trials can be conducted on experimental animals housed in open-circuit respiration chambers, where data are collected on food and water consumption, fecal and urine production, gases of fermentation, and tissue production. In respiration trials, heat loss and energy retention are calculated from oxygen consumption and from production of carbon dioxide and urinary nitrogen. These complex data can be used to determine how energy, carbon, and nitrogen in foods are partitioned and utilized by animals. Digestibility coefficients of foodstuffs are also calculated from these data.

Such rigorous procedures and advanced technology produce extremely useful information. Obviously, however, this quality of information is not often obtained in studies with wild herbivores.

MACRODIGESTION IN CONFINED ANIMALS

Animal Variations and Experimental Design

Variations in the amount of forage consumed in feeding trials have been attributed to season of the year and to the reproductive and production status of test animals. Such differences affect food utilization and should be minimized through experimental design. Between-animal or within-class variations in the way replicates digest a common ration have been reported by many authors. Apparently, as few as three animals, selected because they are similar or identical in size, well-being, production status, tractability, and sex, may adequately depict the apparent digestibility of experimental forages (i.e., provide coefficients of variation of only a few percent). The degree of between-animal variation may also differ by type of herbivore (Van Dyne 1968).

Many ration-herbivore combinations have been tested in digestion trials. The favored statistical designs are the Latin square (Lindahl 1963) and various factorial arrangements (Crampton 1963).

Digestion Trials With Total Excreta Collection

Indigestible residues of ingested food are eventually excreted, but the rate of passage varies widely among animal species. Prior to the actual collection of excreta for chemical analyses, the consumption: excretion relationship must be established. Marker substances in the feed of omnivora and carnivora are recovered in a few hours, indicating rapid passage. However, the large digestive tracts of ruminants may retain a portion of a meal for 1 week or more. Thus, digestion trials on ruminants require at least 2–3 weeks. Some time is needed for stabilizing food intake and for animal reaction; then for 1 week excretory products are collected for analyses. Collected material can be frozen until representative aliquots are prepared for chemical analysis.

Indigestible food residues have been totally collected either with harnesses and bags or in metabolism cages of various designs. Harnesses and suspended collection bags, such as those pictured by Maynard and Loosli (1962, p. 300), have been used with most of the domestic herbivores and with white-tailed deer (Forbes et al. 1941). Animals equipped with collection bags can be maintained in small pens, where some of the rigors and artificialities of very close confinement are removed.

Difficulties with harnessed and bagged animals have also been cited. Stillions and Nelson (1968) noted that the equipment on horses was difficult to keep clean, repair, and adjust, and was cumbersome when the animal was exercised. Forbes et al. (1941) observed that deer sometimes ate their harnesses in apparent attempts to correct the nutritional deficiencies of their test rations. The differential collection of urine and feces from female animals requires intricately engineered collection devices, such as those described by Gorski et al. (1957).

Digestion stalls for steers have been described by Nelson et al. (1954). Special conduits may be harnessed or cemented onto heifers or cows in stalls to provide for the separate collection of urine. Metabolism cages for sheep are pictured in Morrison (1950); stalls for horses are described by Stillions and Nelson (1968); and cages for deer are shown by Cowan et al. (1969).

Most total-collection trials with medium-sized herbivores under dry-lot conditions have been done in metabolism cages. Deer require cage arrangements such as those of Cowan et al. (1969) to minimize disturbance and handling of animals. Feces and urine are allowed to fall through a mesh flooring and are mechanically separated and collected. Perhaps the major difficulty with small digestion cages is the periodic weighing of animals. Even though body weights can be somewhat misleading because animal tissue can be replaced by retained fluids, they are desirable for assessment of animal condition and response to experimental

variables. In digestion trials deer have been housed in individual pens so that they could be shunted into tared weighing boxes on platform scales (Short 1966). However, use of pens without collection devices complicates the collection of feces.

If energy and protein intake are adequate for maintenance, consistent food consumption, excreta production, appearance of excreta, normal behavior, and similar weight at the start and end of the trial are indicators of acceptable experimental technique.

Feed and excreta components analyzed in digestion trials vary with the research objective. Nitrogen, energy, and carbon balances can be determined from digestion trials that measure net energy. Proximal analysis, non-nutritive analyses, or other systems are used to assess the relative value of experimental forages to test animals. The routine analysis of digestion coefficients and calculation of balance data are reviewed in many animal nutrition texts, e.g., Maynard and Loosli (1962); Crampton and Lloyd (1960).

Indirect Methods in Dry-Lot Digestion Trials

When all food eaten and excreta produced is not measured, digestion coefficients can be determined by index procedures. Severe conditions imposed on indicators by Lindahl (1963) include indigestibility and pharmacological inertness. Determination of digestibility coefficients is based on the concentration of the indicator substance in feed and in fecal samples, using the standard equation:

$$\text{Digestibility} = 100 - \left\{ 100 \; \frac{\begin{array}{c}\text{Percent}\\ \text{indicator}\\ \text{in feed}\end{array}}{\begin{array}{c}\text{Percent}\\ \text{indicator}\\ \text{in feces}\end{array}} \times \frac{\begin{array}{c}\text{Percent}\\ \text{nutrient}\\ \text{in feces}\end{array}}{\begin{array}{c}\text{Percent}\\ \text{nutrient}\\ \text{in feed}\end{array}} \right\} \tag{1}$$

Indicators have included chromic oxide, lignin, naturally occurring plant chromogens, and others (Lindahl 1963). Chromic oxide in either a gelatin capsule or an impregnated paper bolus is administered orally, preferably several times daily, to minimize variable excretion rates (McGuire et al. 1966). Digestibility is calculated by procedures described by Crampton and Lloyd (1960). Apparently, the relative accuracy of plant chromogens and lignin as indicators depends on the nature of the forages studied. Errors in indirect methods arise from unrepresentative forage or fecal samples.

Forages Utilized in Digestion Trials

Digestion coefficients obtained from feeding freshly clipped forages in dry lot are meaningful indicators of range forage quality only if the test foods are identical in composition to forages selected by range animals. Range foods have sometimes been modified by being chopped or after clipping by being dried, milled, and pelleted into homogeneous rations that are easy to feed and to sample for chemical analysis. The resulting data represent the processed materials rather than the range plant.

When a foodstuff is incompletely consumed in a digestion trial, the total nutrient intake is obtained either by measuring uneaten orts and subtracting their nutrient levels from those of the offered foodstuff or by combining the orts and fecal fractions. If the animal is allowed to select only the most nutritious portion, the apparent digestibility coefficient will be higher than that determined if the entire food sample had been eaten.

The feeding of concentrates or little-eaten roughages presents special problems because of the small bulk ingested. In such instances, forage digestibility has been determined by difference. First, the apparent digestibility of a basal ration, such as hay, is determined; then that of the concentrate or little-eaten roughage plus the basal ration is decided. The difference in total nutrients apparently digested between the combined and singly fed ration represents the digestibility of the low-bulk item. The major drawback is that the nutrient contribution of the low-bulk item may affect the digestibility of the basal ration.

Rations compounded to simulate a mixture of range forages or a single forage at different phenological stages can be used to predict food quality for herbivores. Such rations generally indicate how certain nutrients are digested rather than the digestibility of a particular plant specimen.

MACRODIGESTION IN FREE-RANGING ANIMALS

Grazing studies can be conducted in small fenced paddocks or on open range. Control over animal variables differs with the experimental situation. The major problems are to determine the quality and quantity of the consumed food and the quantity of the resulting excreta.

Qualitative Estimates of Forage Ingestion

As with closely confined animals, the composition of ingested forage must be known to de-

termine its digestibility. Several approaches have been tried.

Plants have been hand plucked or clipped to provide duplicates of vegetation foraged by tame herbivores or very tractable wild animals.

Hand harvesting provides a first approximation of food quality selected by animals, but such plucked samples frequently vary from forage samples collected through esophageal fistulas. Hand-plucked samples are often of lower protein content and higher fiber content (Bohman and Lesperance 1967).

The nutrient and forage composition of ingested food has been determined through the use of rumen fistulas in range animals. Rumen fistulas are relatively easy to establish and to maintain in domestic animals, and these have been placed in deer several times. Prior to grazing, the animal's rumen-reticulum is emptied through the fistula and even washed out. Thus, recently eaten and little contaminated forage samples are collected for analyses. Since emptying the rumen prior to collecting forage samples disrupts normal digestive processes, animals for qualitative forage sampling are not usually used in concurrent range digestibility trials.

Esophageal fistulation for nutritional studies has been reviewed by Van Dyne and Torell (1964), who described the technique in detail. Such surgically modified animals apparently feed like normal animals, and the forages collected before reaching the stomach can be used to determine both food habits and nutrient composition. Sampling range vegetation by esophageal fistulation is easier and provides a better measure of between-animal variations than does sampling from ruminally fistulated animals (Bohman and Lesperance 1967).

The usual procedures for measuring forage utilization (Forest Service, U.S. Dep. Agr., 1963) provide estimates that are too imprecise for defining either forage components ingested or daily food consumption.

Quantitative Estimates of Range Forage Intake

Forage intake may be estimated from fecal collection data obtained in conjunction with range digestion trials. On homogeneous ranges, excreta is collected from bags attached to grazing animals. Dry-matter (DM) digestion of clipped range plants is determined from standard digestion trials conducted under dry-lot conditions. Feed intake is calculated from weight of bagged fecal material, with the DM eaten: DM excreted ratio obtained in digestion trials. Other forage partitions besides DM have been similarly used to estimate feed intake.

Indigestible indicators contained in the forages and concentrated in the feces are also used to estimate food consumption. In this technique, total indicator concentration in a day's fecal matter is divided by the food indicator concentration: (2)

$$\text{Dry matter consumption (g./day)} = \frac{\dfrac{\text{Units indicator/}}{\text{g. dry feces}} \times \dfrac{\text{g. dry matter}}{\text{in daily feces}}}{\text{Units indicator/g. forage dry matter}}$$

The merits of several indicators, including lignin, plant chromogens, and silica, are described by Van Dyne and Meyer (1964a).

On heterogeneous range, two sets of animals are usually used. The first, esophageally or ruminally fistulated, yields food samples for analysis of internal plant indicators. The second group of animals are equipped with harnesses and collection bags to obtain fecal materials (Van Dyne and Meyer 1964b; Bohman and Lesperance 1967). With wild animals this technique would incorporate the obvious difficulties of maintaining and capturing both groups of animals.

Van Dyne and Meyer (1964b) recently described measurement of forage intake in bifistulated animals. Forage samples collected through esophageal fistulas can be used for determining food habits as well as for nutrient and indicator analyses. Total excreta is obtained daily from fecal collection bags. The digestibility of forage cellulose is determined from 48-hour *in vitro* microdigestion with rumen liquor obtained through a rumen fistula. This information is also measured by inserting forage samples in nylon bags into the rumen through the fistula. Total forage intake per day can then be calculated from the total cellulose excreted per day and the cellulose content of forage samples. Forage cellulose levels are corrected for percent of cellulose digested and not represented in the fecal samples. The advantage of the procedure is that, for cows and sheep, estimates of food ingestion and digestibility can be obtained from one grazing animal. Procedures requiring bifistulated animals probably have little potential for wild herbivores.

Determining Apparent Digestibility of Range Forage

On very homogeneous pastures, freshly clipped forages can be utilized in standard dry-lot digestion trials. On very heterogeneous ranges, the value of this procedure is doubtful, since plants subjectively clipped and freshly fed may not adequately reflect the diet chosen by the animal.

On heterogenous ranges, forage digestibility is measured with naturally occurring and indigestible forage indicators. Apparent digest-

ibility is calculated using equation 1. Feed samples for indicator and nutrient analyses are obtained from esophageally or ruminally fistulated animals, and fecal samples are obtained from collection bags or "grab samples." Various internal indicators have been used to determine the digestibility of a range forage. Lignin was preferred over forage silica by Van Dyne and Lofgreen (1964), and plant chromogens have been advantageous in some studies. However, Bohman and Lesperance (1967) cited results indicating that plant chromogens were unreliable in at least one instance where sheep were grazing on winter range. High concentrations of essential oils in certain plants apparently caused absorption of chromogens, and thereby, distortion of digestibility values. Dietary cellulose was used with some success in a study with mule deer (Short and Remmenga 1965).

Both consumption and digestibility of feed have been estimated with chromic oxide as an external indicator in combination with some naturally occurring plant indicator. The method for calculating digestibility is that of Crampton and Lloyd (1960). Forage intake is estimated from the naturally occurring indicator in feed and fecal samples (equation 2). "Grab" fecal samples are satisfactory for estimates of range forage digestibility from either internal or external indicators. Forage intake estimates, however, require careful determination of total fecal excretion.

Metabolic and Net Energy Determinations

Metabolic energy was calculated for range sheep by Morris et al. (1965). Gross energy was computed from total forage intake, as measured by the lignin ratio technique, and from the mean caloric content of forage samples collected through esophageal fistulas. Energy loss in urine and feces was determined from collection-bag samples; that in gases of fermentation was estimated from data of previous work.

Net energy is determined for grazing animals with the same basic data needed to compute metabolic energy. However, the energy expended on the range also must be measured. For this measurement, an animal that has a tracheal cannula is used (Flatt et al. 1958). Respired gases are collected and analyzed to determine oxygen consumed and carbon dioxide produced. Caloric expenditure is calculated from oxygen consumption, and from production of carbon dioxide and urinary nitrogen. Such determinations compare the quantity of net energy available for secondary production in livestock grazing pastures of varying quality.

MEASUREMENTS OF *IN VIVO* MICRODIGESTION

Scientists have been suspending food samples in the rumen through a fistula for more than 30 years (Barnett and Reid 1961). The advantage of this procedure is that the ruminal environment is probably little changed by the inclusion of such materials, and the complexities of duplicating ruminal conditions, as in *in vitro* studies, are avoided. Samples of several forages can be simultaneously suspended in a single rumen.

Measured quantities of forage or feed are usually placed within porous, indigestible bags. The bags, weighted to submerge in the ingesta, are inserted through the fistula and are attached to the fistula plug to assure retention in the rumen. Van Dyne (1968) reviewed *in vivo* procedures and stated that the retention time needed to maximize microdigestion varies with size, grind, and type of sample. He further noted that the size of bag mesh and the fineness of sample particles may affect loss from the bags. *In vivo* microdigestion data have frequently been closely correlated with macrodigestion coefficients obtained from standard digestion trials.

In vivo microdigestion studies have been conducted with white-tailed deer at Pennsylvania State University. Castrates were more docile than either bucks or does and could be allowed to forage within paddocks or while tethered.

Microdigestion techniques may be useful for estimating digestibility of range-forage samples by wild ruminants. For wild animals microdigestion data have not yet been adequately correlated with macrodigestion data, and little information is available indicating appropriate retention times for bags within the rumen.

SUMMARY

In vivo measurements of digestion are potentially valuable for future Forest Service research. In dry-lot conditions, digestibility of foodstuffs of varied nutrient content can be evaluated. Such data, when used in combination with information about range forage quality and animal habits, will help explain how different herbivore species compete on common ranges.

Range digestibility trials seem destined to be more useful in studies with domestic than with wild herbivores. Maintaining wild animals equipped with excreta collecting facilities and fistulas may prove difficult. *In vivo* microdigestion studies with very tractable specimens tethered or kept in small enclosures could materially increase our knowledge of wild animals.

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Digestibility Trials: *In Vitro* Techniques

HENRY A. PEARSON[1]

Many tons of vegetation are produced and converted to beef, mutton, wool, or venison each year on rangelands throughout the United States. To properly manage these ranges, we measure production, utilization, nutritive value, and digestibility of the forage. Also important to know are the animal requirements for food; supplemental feeding alternatives become important when the food supply is inadequate. Consequently, the range or wildlife manager must (1) measure the value of plants consumed by range animals and (2) measure the animal responses that reflect economic value of the forage. Because of the problems that arise in evaluating the range, much time in research is devoted to development and use of techniques for studying the range forage.

Research concerning the role of the rumen micro-organisms in ruminant animal nutrition dates back to the 1800's and led to the development of the in vitro rumen fermentation technique. This technique has revolutionized the nutritional evaluation of range forage during the last decade. Forage evaluation studies based on this digestion technique involve domestic animals in feedlots and on rangelands, and wild ruminants in cages and in their natural habitat. The literature concerning various phases of *in vitro* digestion work with domestic animals in feedlot studies, is voluminous. Literature on *in vitro* studies for rangelands is not extensive but has increased in recent years. Wildlife studies are limited but will probably increase.

This paper describes the *in vitro* digestion technique, and discusses its usefulness in range and wildlife research. Several recent review publications are available.[2]

PROCEDURE

The *in vitro* fermentation technique simulates under laboratory conditions natural ruminant digestion. The *in vitro* system includes fermentation of a substrate with rumen micro-organisms in a buffered nutrient medium under controlled conditions of anaerobiosis, temperature, and pH. One of two types of system is employed—open or closed. In the closed system, the substrate is fermented in a closed, impermeable container. This container may be a test tube, Erlenmeyer flask, or any other vessel that can be fitted with a suitable closure. Transfers of materials should be minimized. For instance, Rogers and Whitmore (1966) used a vessel with a built-in filter so filtering could be accomplished in the same container as digestion.

The open or continuous-flow system differs from the closed system because a semipermeable or open container is used (Adler et al. 1958, Huhtanen et al. 1954; Louw et al. 1949); this allows addition and removal of metabolities.

Investigators want simplicity in design; therefore, more complicated *in vitro* systems are disappearing. The closed system will be emphasized in this paper since it is universally used because of its simplicity.

Substrate

The amount of substrate or sample to be evaluated varies (0.25–1.0 g.) in different laboratories (Barnes 1967). Within limits, fineness of grind does not affect digestibility if the samples are ground finely enough to insure good sampling of the small weights of herbage used (Tilley and Terry 1963). The limits of fineness are exceeded when samples are ground very fine by ball milling or as large as 2.5 millimeters (Dehority and Johnson 1961; Minson and Milford 1967). Fine grinding by ball milling was assumed to disrupt the cell walls of the plant structure, while the large particles were apparently not digested completely. Van Dyne (1962) indicates a maximum particle size of 1 millimeter for *in vitro* digestion work. No difference was found in drying samples at either 40° C. or 100° C. compared with freeze drying. Drying at 100° C. has a marked effect only if continued longer than 4 days (Tilley and Terry 1963).

Buffer and Nutrient Media

The artificial saliva or buffer solution generally used (McDougall 1948) contains phosphate-bicarbonate buffers, which are saturated with carbon dioxide. The basis for this solution has been the chemical analysis of sheep saliva. There have been alterations, additions, and subtractions for individual laboratory techniques. For instance, urea, glucose, vitamins, or other growth factors are added to the basic nutrient medium (Donefer et al. 1960; Johnson 1966). A relatively large volume of buffer

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[2] Bruggemann et al. 1968; Dougherty et al. 1965; Hungate 1966; Johnson 1966; Van Dyne 1962.

solution (40 ml.) is used; use of so much solution usually insures that the final acid concentration does not exceed that found in the animal (Tilley and Terry 1963).

Inoculum

The *in vitro* system utilizes undiluted or only slightly diluted rumen liquor, whole liquor diluted with mineral solutions, or various fractions of rumen liquor such as centrifuged cells or washed cell suspensions. Several investigators have discussed these various inoculum preparations (Johnson 1963; Shelton and Reid 1960; Van Dyne 1962). Aeration of the rumen liquor inhibits micro-organism activity by 40 percent in 15 minutes and by 100 percent in 30 minutes (Johnson et al. 1958).

Questions have been raised concerning the validity of using the inoculum from an animal fed on a different kind of feed than the feed being evaluated. Several workers who have studied this subject recommend that the inoculum source animal either be fed on the same forage to be evaluated, or be fed a standard forage that is analyzed simultaneously with other forages and used as a correction factor.[3] In our laboratory, we have found differences in forage digestibilities due to inoculum collection delays where inoculum source animals were grazing the same range species being analyzed but during a different vegetative growth period (Pearson 1967a).

We investigated the effect of analyzing native range species with inoculum from animals grazing introduced species, and vice versa. In vitro digestibilities of six forage species and a diet mixture from ponderosa pine range were determined with inoculum from animals grazing native and introduced species. Analysis of variance revealed no overall difference in the forage digestibilities due to inoculum source (table 1), but examination of the individual digestibility samples revealed differences of up to 10 percent. Apparently the species-inoculum source interaction variance was sufficiently high to mask any significant individual differences.

Careful examination of the individual interactions reveals that *Festuca arizonica* and *Muhlenbergia montana* had higher *in vitro* digestibilities when inoculum source animals grazed native range, while *Agropyron intermedium* and the diet mixture, 65 percent of which consisted of introduced species, were lower. Other species responded differently between dates. Since individual values are important, these results substantiate use of inoculum from animals grazing the forage to be analyzed. Other inoculum sources may be used only after information has been obtained concerning digestibility variances.

[3] Van Dyne 1962 Bezeau 1965; Johnson 1966; Bruggemann et al. 1968.

TABLE 1.—*Percent digestibility of forages collected from pine ranges and digested with inoculum from animals grazing native and introduced species*

Forage	Inoculum source: Introduced species	Inoculum source: Native species
June 1967:		
Festuca arizonica	56.8	59.7
Muhlenbergia montana	43.6	53.1
Sitanion hystrix	64.4	62.9
Carex geophila	54.1	57.1
Agropyron intermedium	67.5	60.0
A. cristatum	60.7	62.7
Diet mixture	66.4	59.6
August 1967:		
F. arizonica	51.3	52.4
M. montana	57.8	58.2
S. hystrix	65.2	65.7
C. geophila	61.3	55.4
A. intermedium	62.0	61.6
A. cristatum	60.0	59.2
Diet mixture	57.0	52.4

Rumen fluid containing micro-organisms was frozen to preserve inoculum for delayed forage digestibility trials. Trials using frozen and fresh inoculum indicated that the micro-organisms die or at least become inactive since digestibilities using frozen inoculum are lower (table 2).

TABLE 2.—*Percent digestibility of forces collected during January 1966 on chaparral range. Forages digested with fresh and frozen inoculum, with and without carbon dioxide flushing, prior to tube closure*

Forage	Treatment: Fresh inoculum, CO_2 flush	Treatment: Frozen inoculum, CO_2 flush	Treatment: Fresh inoculum, not flushed
Ceanothus greggii (leaves)	47.9	41.2	31.9
Quercus turbinella (leaves)	44.6	36.3	37.8
Cercocarpus breviflorus	34.6	30.2	35.7
C. greggii	31.6	25.2	17.4
Rhus trilobata (stems)	41.7	35.2	21.7
Poa longiligula	52.6	37.9	47.8
Sitanion hystrix	48.9	32.6	47.1
Eragrostis lehmanniana	39.5	18.8	21.9
Bouteloua hirsuta	38.8	19.4	29.4
B. gracilis	31.9	15.2	27.5
Diet mixture (steer 3)[1]	32.1	20.8	32.6
Diet mixture (steer 4)	27.3	26.1	16.1
Mean[2]	39.3a	28.2b	30.6b

[1] Diet mixture refers to forages removed from the rumen of cattle in rumen evacuation trials.

[2] Means with same letter in common are not significantly different at the 0.1 significance level.

The inoculum should be kept in anaerobic conditions throughout the digestion process. This is generally accomplished by one of two techniques: (1) continuous flushing with carbon dioxide or some other suitable gas during the entire digestion period (Van Dyne 1962) or (2) initial flushing with gas and closure of the digestion tubes with closures that provide for gas release (Tilley and Terry 1963). In the latter method, the initial flushing to displace the oxygen prior to closure is essential for maximum fermentation (table 2).

Length of Fermentation

Fermentation time varies among individual laboratories; most universal time lengths are 12, 24, and 48 hours fermentation by the micro-organisms; however, many other fermentation times have been explored. Differences in digestion have been significant, especially in the shorter digestion times. Dry-matter digestion increased with increasing length of fermentation up to the 48 hours tested in our laboratory (fig. 1). Similar results have been reported in other laboratories. Addition of acid-pepsin solution will increase digestion for various lengths of time. Tilley et al. (1960) used 48 hours of acid-pepsin digestion, while Barnes (1966) used 24 hours. Differences in digestibility between these two time lengths are small (table 3), therefore either time length can be used effectively.

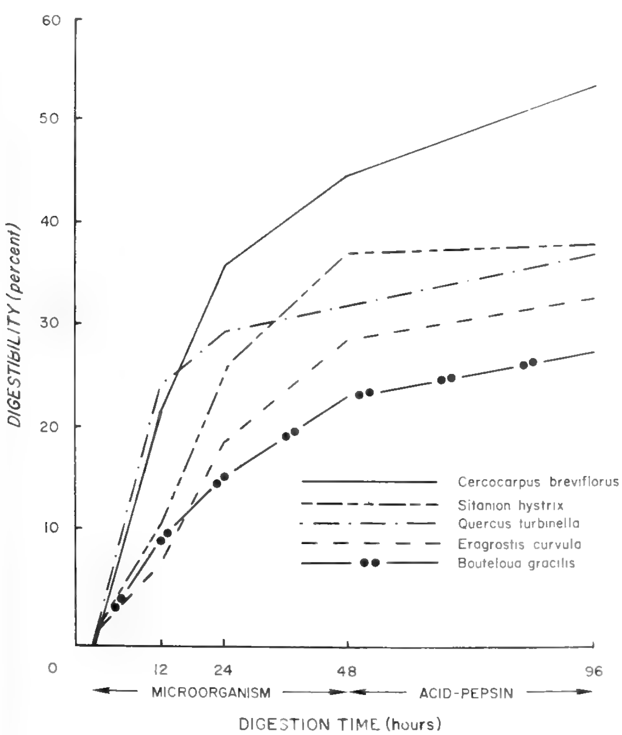

FIGURE 1.—Rates of in vitro dry matter digestion with rumen inoculum, plus additional acid-pepsin digestion.

TABLE 3.—*Percent forage digestibility when using 24 and 48 hours acid-pepsin digestion in the two-stage technique (Tilley and Terry 1963). Forages were collected from the chaparral range during November 1966*

Forage	Hours 48	Hours 24
Quercus turbinella (stems)	24.0	23.4
Ceanothus greggii (stems)	24.3	25.8
Cercocarpus breviflorus (stems)	32.5	32.3
Rhus trilobata (stems)	41.5	37.7
Q. turbinella (leaves)	47.7	44.5
C. greggii (leaves)	44.5	45.0
C. breviflorus (leaves)	54.0	51.5
Diet mixture (steer 6)[1]	37.6	36.0
Diet mixture (steer 4)	51.0	48.4
Sitanion hystrix	57.2	56.9
Bouteloua curtipendula	41.7	40.4
Eragrostis lehmanniana	51.1	48.3
E. curvula	43.0	41.0
B. hirsuta	46.7	44.9
B. gracilis	44.5	42.2
Mean	42.8	41.2

[1] Diet mixture refers to forages removed from the rumen of cattle in rumen evacuation trials.

Forage digestibilities obtained with various lengths of micro-organism fermentation have been attributed to different aspects of nutrition. For instance, digestibilities with short periods of fermentation appear related to the rate of voluntary intake by animals, while long periods describe forage digestibility.[4] The leveling off of rumen micro-organism activity with long periods of fermentation, which describes forage digestibility, has been attributed to the effect of lignin. Apparently lignin in forages is a physical barrier to the rumen micro-organisms.[5]

Digestion Components

Various components in forage are known to be (1) water soluble, (2) digested by micro-organisms, or (3) digested by acid-pepsin. Forage samples are processed by three methods to ascertain the amounts of each of these three components. The water-soluble portion is dissolved in buffer solution for 48 hours; digestion for 48 hours in buffer solution plus rumen inoculum dissolves those portions of the forage that are water soluble or digestible by micro-organisms; and further digestion in acid-pepsin for 48 hours dissolves that portion digested by acid-pepsin. Average *in vitro* dry matter digestibilities for chaparral forages collected in May were: Water soluble, 20.9 percent; micro-organism digested, 21.9 percent; and acid-pepsin digested, 7.0 percent. Thus, total digest-

[4] Barnes 1966; Crampton 1957; Crampton et al. 1960; Donefer et al. 1960.

[5] Dehority and Johnson 1961; Dehority et al. 1962; Kamstra et al. 1958; Sullivan 1959.

ibility was 49.8 percent (table 4). Although variations due to season, location, and species would be expected, similar evaluations and results were reported in Indiana by Barnes (1966).

Digestibilities determined with micro-organisms and micro-organisms plus acid-pepsin were highly correlated ($r=0.971$, $p<.01$), which indicates the interchangeable predicting value of either method. Digestibilities determined only with buffer were not significantly correlated with digestibilities from either of the other methods; consequently, the water-soluble component in forage apparently has no value in predicting forage digestibility.

TABLE 4.—*Comparison of percent in vitro dry matter digestibility methods, determined on chaparral forage collected during May 1966*

Forage	Methods		
	Buffer	Buffer + micro-organisms	Buffer + micro-organisms + acid-pepsin
Grasses:			
Bouteloua curtipendula	15.2	35.4	41.8
B. gracilis	17.0	42.0	47.6
B. hirsuta	14.7	38.8	46.2
Eragrostis curvula	14.2	40.7	49.2
E. lehmanniana	16.1	43.3	54.3
Sitanion hystrix	21.4	59.8	69.5
Brush:			
Cercocarpus breviflorus	24.9	41.0	46.0
Ceanothus greggii	22.0	36.1	41.6
Quercus turbinella	30.5	38.4	45.7
Rhus trilobata	33.9	43.5	49.9
Diet mixtures			
Steer 4	21.3	44.8	49.1
Steer 6	19.2	50.3	57.0
Mean	20.9	42.8	49.8

A Standard Method

In vitro digestion is a relatively new tool, and several techniques are used at various laboratories. One standard method of relating data from different laboratories is urgently needed. At the Tenth International Grassland Congress in Finland, several papers were presented concerning *in vitro* digestion.[6] All these papers indicated use of a two-stage technique described by Tilley and Terry (1963), either as standard procedure or for comparison. Barnes (1966) and Tilley et al. (1960) indicated that the two-stage technique is the most reliable method for estimating *in vivo* forage digestibility. Van Soest (1967) also considered this technique superior to other in vitro techniques because it involves essentially an enzymatic preparation of undigested cell walls. In application, the two-stage technique has been used to relate digestible forage consumed to beef production (Pearson 1967b). Although many scientists apparently think this technique approaches the answer as a standard method, it was not included in collaborative studies to investigate possibilities for a standard method (Barnes 1967). Perhaps these collaborative studies were initiated prior to knowledge of the value of the two-stage technique.

In Vitro Techniques Used at Flagstaff, Ariz.

Since the two-stage *in vitro* method is frequently employed, and is the method used in our laboratory, the procedure used, with various modifications, will be outlined here.

The equipment and reagents used include:

Equipment	*Reagents*	
Forage grinder or mill	Buffer solution:	
Drying oven	*Ingredient*	*g/liter H_2O*
Analytical balance	$NaHCO$	9.80
	$Na_2HPO_4 \cdot 7H_2O$	7.00
Thermos	KCl	.57
	$NaCl$	.47
Digestion containers (100-ml. centrifuge tubes).	$MgSO_4 \cdot 7H_2O$	.12
	$CaCl_2$	.04
Incubator (water bath)	Carbon dioxide gas	
pH meter	Hydrochloric acid solution (one part HCl) (11.6N); four parts H_2O)	
Vacuum filter apparatus		
Automatic pipetter	Sodium carbonate (53 g/liter H_2O)	
	Pepsin (1:10,000) 0.12 g/5 ml. H_2O	

Whole rumen liquor is removed from rumen-fistulated cattle (fig. 2) grazing the range forages to be evaluated. The rumen ingesta is

FIGURE 2.—Rumen fluid for in vitro digestion trials is obtained from fistulated cattle.

[6] Barnes 1966; Dent and Aldrich 1966; Noller et al. 1966; Van Soest et al. 1966; Wedin et al. 1966.

strained through cheesecloth into a prewarmed insulated thermos (1–2 gallons depending upon need). The thermos is completely filled to eliminate air. Several subsamples are taken from different parts of the rumen. When available, several animals are sampled and the rumen liquor mixed. The inoculum-source cattle are trapped at dusk, held off feed overnight, and sampled the following morning. Alexander and McGowan (1966) illustrated the small variation in activity of rumen liquor due to the effect of inoculum extraction related to feeding. They also demonstrated no real differences in rumen inoculum activity related to animal variances. Therefore, inoculum could be used from a single animal or as a mixture from several animals.

The *in vitro* digestion laboratory procedure is as follows:

Step I:

1. Grind dried forage samples to pass a 0.5 mm. screen. Redry ground samples for 4 hours at 100° C.
2. Place triplicate 0.5-gram (±0.1 mg.) samples into 100-ml. digestion tubes. Include empty reagent check tubes in each digestion trial.
3. Saturate buffer solution with carbon dioxide to pH 6.8 by bubbling, and warm to 38.5° C.
4. Add whole rumen fluid strained through cheesecloth to buffer solution (one part rumen fluid to four parts buffer solution).
5. Add rumen fluid-buffer solution mixture to digestion tubes containing forage samples (50 ml./tube).
6. Immediately exhaust air in remaining space above the liquid in the tube with carbon dioxide, and insert closure. The closures are stoppers fitted with an exhaust valve to permit escape of gases within the tube during fermentation, and yet prevent reentry of air into the tube (Tilley and Terry 1963).
7. Incubate 48 hours at 38.5° C. (fig. 3).
8. Shake tubes individually to mix forage initially and 2, 6, and 24 hours after start of incubation.

FIGURE 3.—Water bath used for incubation during an in vitro fermentation trial.

Step II:

1. Add 4 ml. of HCl solution to reduce to pH 1–2 (acid added in four ½-ml. doses and two 1-ml. doses to prevent excess foaming).
2. Add 5 ml. of pepsin solution and close tubes.
3. Incubate 48 hours at 38.5° C.
4. Shake tubes individually to mix forage initially and 2, 6, and 24 hours after the start of incubation.
5. Add 12 ml. of sodium carbonate solution to stop enzymatic action.[7]
6. Vacuum filter,[8] dry, and weigh.

Since many digestion tubes may be used simultaneously and since filtration may extend over a long period step 5 has been added to stop enzymatic action in all tubes at the same time. Pepsin becomes inactive at about pH 4.6, and is readily denatured at pH value higher than 6; optimum activity occurs at approximately pH 2 (Fruton and Simmonds 1958). Digestibility is similar whether the substrate is filtered immediately following digestion, or whether it is delayed after the addition of so-

[7] This step is optional. Whether it is taken depends on the number of tubes to be filtered

[8] Grade GFA Whatman glass fiber papers (fiber diameter < 1 micron) are used.

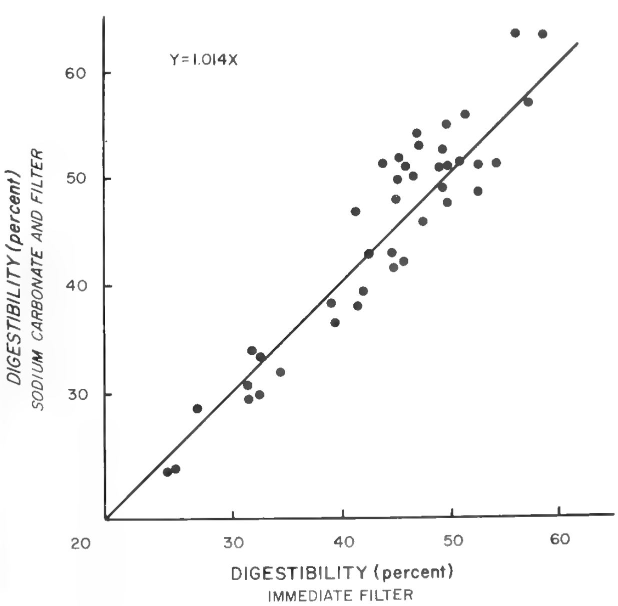

FIGURE 4.—Comparison of immediate filter after in vitro digestion and delayed filter after adding sodium carbonate to stop enzymatic action.

dium carbonate (fig. 4). The filtering process was first described by Alexander and McGowan (1961).

All *in vitro* digestion data are recorded on automatic data processing forms. Fortran computer programs are used to compile individual dry-matter digestibilities and triplicate tube digestion summaries.

USEFULNESS

Digestibility

The usefulness of the *in vitro* fermentation technique in evaluating forages must be judged by the accuracy with which it can predict the value of the forage to the animal. *In vitro* fermentation results are usually reported in terms of digestible dry matter or digestible cellulose. Van Soest (1967) cautioned researchers against using only one component, such as protein, cellulose, or crude fiber, to predict digestibility, since all nutrient digestibilities should be included in such evaluations. These component digestibilities are, in turn, related to *in vivo* measurements such as total digestible nutrients (TDN), digestible dry matter (DDM), digestible energy (DE), and several other measures of feed value (Baumgardt et al. 1962a, 1962b; McCullough 1959; Moir 1961). Most workers have not related *in vitro* fermentation values directly to animal responses, but it appears that *in vitro* values should be evaluated by their correlation with animal production, rather than by their correlation with other laboratory measures. *In vitro* digestion research has attempted to estimate *in vivo* values, which are themselves only estimates of animal production. These *in vivo* measurements are also meaningless without direct or inferred relationships to animal production.

In vitro digestible forage consumed was related to yearling Hereford cattle gain on ponderosa pine ranges from 1963 to 1967. These preliminary data indicate that the relationship can be expressed as a straight line:

$$Y = -1.013 + 0.257X$$

where X is in vitro digestible dry matter consumed in pounds per acre and Y is beef gain in pounds per acre (fig. 5).

In vitro techniques can be used to evaluate the nutritive value of forage consumed by both domestic and wild animals (Short 1963). Plant fractions—leaf, stem, and seed—can be evaluated by this method (Pearson 1967b). Plant breeders can evaluate the nutrition of newly developed strains and varieties. The effect of management practices and the effect of fertilizers and herbicides can also be tested.

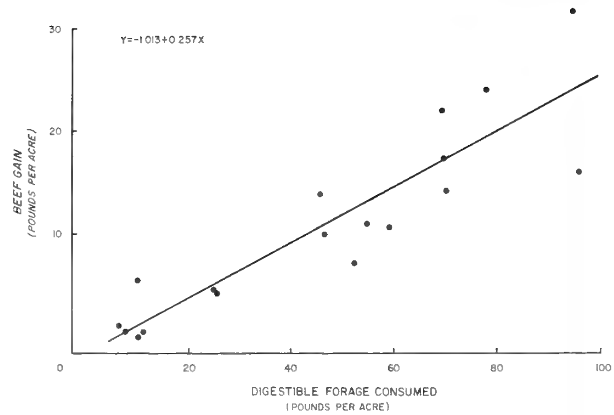

FIGURE 5.—Beef production as related to digestible forage consumed.

Volatile Fatty Acids

Another phase of *in vitro* work is evaluating the volatile fatty acids produced by various feeds. Rice et al. (1962) in Wyoming related *in vitro* volatile fatty acid production to the feeding value of forage as expressed by conventional TDN determinations. Knowledge of the volatile fatty acids produced could help in determining the type of feed needed for a particular purpose. For instance, feeds that produce low proportions of acetic acid in the rumen will yield milk of low fat content but will show a high feed conversion to milk (Tilley et al. 1960). Rations high in production of propionate and butyrate may be expected to result in more efficient fat production than rations high in acetate (Shaw 1959). From analyses of volatile fatty acid and gas composition during in vitro fermentations, Short (1963) demonstrated that deer and cattle utilize an alfalfa-corn diet similarly, but that browse species were digested better by deer. Nagy et al. (1967) compared the inoculum from deer, cattle, and sheep to determine their ability to digest alfalfa hay, and found all similar in volatile fatty acid production when the animals were on an adequate diet.

Intake

To determine the value of a feed, we must know both its digestibility and the amount of forage an animal consumes voluntarily. Recent research has indicated that this aspect of nutrition may be evaluated by *in vitro* fermentation trials.[9] As indicated earlier, short periods of digestion—6 to 12 hours—are best related to intake. This theory hypothesizes that the speed at which a particular forage is digested and re-

[9] Crampton 1957; Crampton et al. 1960; Donefer et al. 1960; Barnes 1966.

moved from the rumen determines the animal intake of that forage. Although no relationship has been shown from data collected in our laboratory, confirmation of a direct relationship between *in vitro* fermentation and voluntary intake would open a new field in nutrition work. This relationship would be especially beneficial to range and wildlife research because of the difficulty in determining feed intake by range animals. A procedure for determining forage intake, based on *in vitro* and *in vivo* microdigestion, has been described (Van Dyne and Meyer 1964). This procedure utilizes the conventional method but substitutes microdigestion for conventional macrodigestion determinations of the forage.

SUMMARY

In vivo digestibility experiments are of great importance in estimating the nutritive value of forages to ruminants. These experiments are tedious and require large amounts of forage. Because of simplicity, speed, precision, and economy, attention has turned to *in vitro* fermentation studies for estimating the nutritive value of forages. Although some disadvantages are apparent, mainly the lack of standardized methods, the *in vitro* fermentation technique will be extensively used and may become the accepted method for analyzing the nutritive value of forage for domestic animals and wildlife.

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DETERMINING ANIMAL CONSUMPTION

Relating Vegetation Measurements to Forage Consumption by Animals

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The productivity of range animals depends largely on the quality and quantity of the forage they consume. The focus of this conference is on habitat evaluation—with emphasis on how well range forage meets the needs of range animals. Therefore, proper evaluations must include animal performance. We can weigh livestock at intervals to determine rate of gain. However, if the animals have had access to several kinds of forage, we cannot know, from weights alone, which kinds of forage were responsible for the observed gain. Several methods of observing animals, their stomach contents, or their excreta—to determine kinds and relative quantities of forage eaten—are evaluated elsewhere in this publication. However, data points are so difficult to obtain by these methods that the scope of such measurements usually is severely limited. The purpose of this paper is to explore the possibilities of determining the quality and quantity of the forage animals eat by observing or measuring forage plants.

METHODS OF MEASURING FORAGE PRODUCTION AND UTILIZATION

Most methods for estimating production and utilization of range forage were developed to improve range management decisions. These methods have provided workable guides for stocking the range. Their relative merits as management tools have been discussed in previous meetings and will not be reviewed here. Rather, the question is whether vegetation measurements can be used to determine when, what, and how much a grazing animal ate.

Methods of estimating herbage production were reviewed by Reppert et al. (1962). Forage production on range units may be measured by the weight estimate method (Pechanec and Pickford 1937), some modification including double sampling (Wilm et al. 1944), or by clipping and weighing forage from sample plots or transects.

Smith et al. (1962) classified utilization methods as: (1) Methods based on differences before and after grazing or between grazed and ungrazed plots or plants; (2) methods based on measurement, correlation, and regression of factors related to utilization; and (3) methods based on general observations and comparisons with predetermined standards of use. For administrative use, ocular estimates (Reid and Pickford 1941), methods based on height-weight relationship, as recommended by Lommosson and Jensen (1943) and various grazed-plant-count methods (Roach 1950; Springfield 1961; Gierisch 1967) have been reasonably satisfactory. Actual weight methods that require movable cages have been popular in pasture and intensive range studies.

Difference Methods

One approach to estimating consumption is to estimate or measure the amount of herbage on marked plots at the beginning and end of each grazing period. The major problems are to account for nonrelevant utilization and for growth. If these limitations are recognized, ocular estimates on the same plots before and after grazing can provide clues to animal consumption in range and wildlife habitat research.

Cages are commonly used in estimations of production and utilization of forage on small, intensively managed, improved pastures where forage yields of 3,000 to 5,000 pounds of dry matter per acre are common. One objection to the use of cages is that they modify the microclimate. However, changes in the microclimate due to caging were fairly small, with the use of open-mesh wire cages on annual range in California (Heady 1957).

Using three variations of the clipped-plot method, where yields averaged 4,000 pounds

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per acre, Nevens (1945) found that subtracting the yield of the grazed plots for the previous period from the current yield of the caged plot gave the best results.

The Joint Committee of the American Society of Agronomy, American Dairy Science Association, and the American Society of Animal Production (1943) recommend two movable-cage procedures: (1) Paired caged and grazed plots are both clipped to ground level at the end of each grazing period to obtain consumption by difference, or (2) the caged plot is hand plucked at the end of each grazing period to match use on the grazed plot. Both procedures require a new set of caged and grazed plots for each grazing period. Usually the first plot of each pair is chosen at random; and a second plot, nearby and similar to the first, is then chosen as its mate; the plot to be caged is then determined by flipping a coin (Klingman et al. 1943).

The reliability of caged plots, paired with grazed plots, for determining herbage yield was evaluated by Klingman et al. (1943). On a 12-acre pasture where the average yield of forage was 650 to 700 pounds per acre, 308 singly placed pairs of 4-foot-square plots were needed to estimate dry matter with a standard error of 50 pounds. Only 12 pairs of plots were needed for a standard error as large as 250 pounds. These values suggest the intensity of sampling needed in intensive grazing studies to estimate gross herbage production or consumption. The variability involved in most range management and wildlife habitat research probably is greater than that in Klingman's study.

Grazed-Plant Methods

Various adaptations of the grazed-plant method are used for determining grass utilization on rangeland. Usually 100 tufts are observed, and a previously developed regression curve is used to convert the number not grazed to an estimate of percent utilization. One shortcoming of the grazed-plant method is that cattle may graze without changing the percentages of grazed and ungrazed plants, by regrazing some plants close to the ground, and by leaving ungrazed plants of the same species untouched (Zemo 1968).[2]

Another deficiency of the grazed-plant method is that, to estimate consumption, it must be used in conjunction with some other method that measures production. Consequently, production and utilization are not measured on the same plants.

The counts in plant-count methods are binomially distributed. For example, a sample of 250 tufts is needed for a confidence interval within 20 percent of the mean if 30 percent of the plants are ungrazed. If fewer than 30 percent of the plants are ungrazed, more than 250 plants must be observed for the same precision.

Sampling Errors

Green (1952) found the coefficient of variation for herbage production to be between 20 and 35 percent when the yield lay between 1,000 and 2,500 pounds of dry matter per acre and sample units were 1 or 2 square yards. With yields as small as 500 pounds, as on grazed areas, the coefficient rose to 60 or 80 percent. Sampling variation associated with grazed residues was high, partly because of low yield. Where estimates of dry matter consumed within 2 to 3 weeks ranged from 3,000 to 200 pounds, the maximum standard deviations ranged from 700 to 500 pounds per acre at the highest and lowest mean values, respectively. Thus, while the coefficient of variation was 23 percent at 3,000 pounds and 250 percent at 200 pounds per acre, the absolute value of the standard deviation was almost as great where consumption was 200 pounds per acre as it was at 3,000 pounds. Standard deviations of 500 pounds per acre are greater than we like —perhaps too great to be useful—on ranges of low productivity. Larger sample units will sometimes reduce plot-to-plot variations to an acceptable level.

Use of permanent plots is supposed to eliminate the additional sampling error encountered when new sample plots are selected. This advantage is partly offset because the mean from a set of randomly selected permanent plots may differ greatly from the pasture mean. The combined data for several short grazing periods, using new plots for each period, may give more accurate averages than would be obtained from repeat measurements on a single set of plots. Nevertheless, repeated measurements on permanent plots provide an index to relative changes in the amount of forage on a given range unit with less effort than it can be obtained by choosing new plots each time.

A major deficiency of permanent plots is that they cannot be clipped to measure herbage yields. Therefore, forage production and utilization must be estimated. Ocular estimates are both tedious and subjective. However, instruments that accurately and rapidly measure dry matter without disturbing the vegetation are being developed. Such instruments may eliminate ocular estimates. They may even eliminate the need for permanent plots.

[2] Zemo, Tesfay. 1968. Behavior and grazing preference of fistulated steers on a desert grassland. (Unpublished master's thesis on file at the Univ. Ariz., Tucson, Ariz.)

FACTORS AFFECTING UTILIZATION

The consumption of a given species per animal on any part of a range unit depends on how accessible and desirable that species and part of the range are to the animal, and on the relative abundance of associated species.

The degree of utilization on pine bunchgrass in northern Arizona was related inversely to distance from water and to steepness and length of slope, but positively related to proximity to trails and other access routes (Glendening 1944). Mueggler (1965) found a negative exponential relation between accumulated relative use and distance upslope from the bottom of the slope. In an evaluation of 21 factors, Cook (1966) found that 11 were significantly related to utilization of mountain slopes by cattle. He concluded, however, that utilization on a given part of the range could not be predicted from the relationships studied. On a desert range, Cook (1962) found that the average percentage of utilization for each of seven species was related to such factors as: (1) Averaged weighted percent use for all species, (2) utilization on the more palatable species, (3) utilization on the less palatable species, and (4) the relative abundance of each forage species present. Clearly, the relationships that determine consumption of a given species by a given animal at a given time and given place are complex.

SOME FACTORS AFFECTING UTILIZATION MEASUREMENTS

Seasonal Variations in Forage Growth

The problem of relating utilization of forage to animal consumption is complicated by species differences in seasonal rate of growth and in response to grazing. In Wyoming, Lang and Barnes (1942) found that short grasses and perennial forbs produced more forage when harvested frequently at ground level than when protected during the growing season and harvested after growth stopped. Midgrasses and annual forbs produced more forage if harvested at the end of the growing season. In California, on annual range, Ratliff and Heady (1962) found that the periods of most rapid growth extended from March 28 to April 24. Early in the season, filaree and burclover were the most rapid growers, then wild oats and ripgut, next soft chess, and finally ryegrass. In Arizona, on the Santa Rita Experimental Range native perennial grasses produced 93 percent of the year's growth in about 9 weeks, mainly in July and August (Culley 1943).

Invisible Utilization

Past utilization on rapidly growing plants may not be measurable because evidence of grazing or browsing has been obscured by regrowth.

Another kind of invisible utilization is that of plant parts that are pulled out rather than cut off. Young basal leaves and their sheaths on grasses such as little bluestem often are pulled out, leaving the broken surfaces hidden by old sheaths. Immature seedstalks of many grasses disarticulate within the sheath, and flower stalks of some low-growing forbs have their weakest point at or below ground level. Flowers of these plants can be grazed without leaving visible stubble.

A third category of invisible utilization is the consumption, in season, of deciduous materials. These include many kinds of fruits, leaves of deciduous shrubs, and entire seedheads of some grasses. Once the deciduous plant part has fallen, the amount taken by livestock cannot be estimated.

Plants pulled up by the grazing animal constitute a fourth category of invisible utilization. However, steers on the Santa Rita Experimental Range usually discard annual grasses that are uprooted (Zemo 1968).[3]

Errors introduced by invisible utilization have not been studied extensively. At this point, about all we can say is that they do exist and should be measured if there is a chance that they will seriously reduce forage consumption estimates.

Extraneous Utilization and Disappearance

An opposing source of error, i.e., one that may bias forage consumption estimates upward, is that of distinguishing between forage consumed by study animals and losses to other influences. Most ranges support unmeasured populations of big game, small mammals, birds, and insects. It may be impossible to distinguish between the grazing or browsing of domestic livestock and that of other animals. Apparent consumption also can result from: (1) Trampling that damages rapidly growing tender plants and reduces forage yields, (2) normal losses of deciduous plant parts, and (3) losses due to wind, hail, or the cutting action of sandstorms. Available forage declines as plants mature, cast seeds, shed leaves, and are broken up or flattened out by the weather. Some leaching of soluble materials also occurs.

RELATING PLANT AND ANIMAL MEASUREMENTS

In grazing studies, animals are used not only to obtain a desired experimental condition, but also to measure sward performance (Lucas 1962). Animal weight gain, adjusted for energy spent in gathering forage or added in sup-

[3] See footnote 2, page 94.

plemental feed, is the usual standard against which vegetation measurements are evaluated. The amount of forage consumed per animal can be a dominant factor controlling production per animal. In fact, Crampton et al. (1960) report that the relative importance of forage intake and forage digestibility in determining rate of gain are 70 and 30, respectively. Animal performance always responds to changes in forage yield and quality, but it is a trustworthy index only if other factors conditioning the relationship are standardized or can be properly evaluated.

Observations of Hereford and Santa Gertrudis cows in New Mexico showed that they ate some of all available species, and that there was no apparent difference between breeds (Herbel and Nelson 1966). Cook et al. (1962) found that the daily intake of forage was less on poor ranges than on adjacent good ranges, and that the daily intake from both good and poor ranges decreased as utilization reduced available forage. In a related study, Cook, Kothmann, and Harris (1965) found that total protein, ash, lignin, and other carbohydrates were somewhat higher in forage selected by sheep from poor ranges; that ether extracts, cellulose, and gross energy were higher in forage from ranges in good condition; and that the digestibilities of cellulose and other carbohydrates and gross energy in the forage from both good and poor ranges decreased as utilization increased. The amount and quality of forage available can influence forage intake more than the animals' forage preference. Decreases in forage intake and quality as forage becomes scarce may also increase the ratio of forage consumption to animal gain. Because of these factors, it is hazardous to estimate forage consumption from animal gains.

Relation of Apparent Forage Consumption to Animal Gain

Evans et al. (1962) state that the meaningfulness of herbage weights is questionable because of the rapid changes in vegetation, and they stress the need for rapid weight inventory methods. Linehan and Lowe (1946) found that total output, as measured using the movable cage method, differed from that based on animal weighings by only 6.8 percent. The coefficient of correlation for the two kinds of yield estimates was 0.88. Grazing periods ranged from 7 to 23 days. Excessively frequent clipping in periods of rapid herbage growth was a major source of error in the movable-cage method.

In a later study, Linehan (1952) reported that clipping procedures were accurate enough where the herbage on highly improved 2-acre study paddocks was grazed down in 3 days, the cattle moved, and clippings taken of the uneaten herbage. However, on pastures grazed season long under the farmer's control, the same clipping schedule gave low accuracy. On farmer-controlled areas, the sward was overdefoliated in the spring, it accumulated heavily in the flush period, and the accumulation was not consumed until near the end of the season.

Morrison and Ely (1946) estimated the TDN (total digestible nutrients) per acre by clipping at 1,578 pounds, compared to 2,305 pounds as computed from animal weight gains. Herbage was clipped with a lawnmower set at 1 inch, and caged plots were mowed at the end of each grazing period. Wagner et al. (1950) compared the use of six 4- by 4-foot cages with four mower strips 3 by 30 feet, clipped at 2 inches before the cattle were turned in. Average TDN yields of 3,500 to 4,000 pounds per acre were recorded. They found that the strips gave yields of TDN that more closely approximated computed TDN intake of animals grazed. When the cage method was used, yields of both bluegrass and orchardgrass were overestimated. Grelen (1967), using plots 3.1 feet square protected by cages 4 feet square, also found that stationary cages overestimated yield.

Most attempts to relate herbage measurements to forage consumption have involved areas of 10 acres or less and herbage yields of 2,000 to 4,000 pounds per acre. Most attempts have also involved grazing periods of 3 days to 6 weeks, and nearly complete harvesting of the forage during the grazing periods. In these tests, forage-consumption estimates derived from adjusted animal weight gains have been the standard against which consumption estimates based on vegetation measurements were evaluated. Actually, animal weight gains may provide very poor estimates of forage consumption. This is especially true under range conditions where animals may travel several miles from water to forage, where external and internal parasites and other factors have unmeasured impacts on the animal, where grazing periods range from a few weeks to several months, where many kinds of forage are available, and where the plane of nutrition varies seasonally from submaintenance to adequate.

Herbage Production and Consumption on Semidesert Range

Since 1954 records of herbage production and utilization have been maintained for the 16 major pastures on the Santa Rita Experimental Range.[4] On about October 1 of each year

[4] Maintained by the USDA Forest Serv., located 30 miles south of Tucson, Ariz.

herbage production of annual and perennial grasses is estimated on the same plots. Temporary plots are used to establish relationships between estimated and actual herbage yields. Individual plot sizes range from 9.6 square feet (where herbage production is relatively high) to 192 square feet, where production is low. In June utilization of perennial grasses is estimated at each herbage production plot, using the ungrazed plant method (Roach 1950). These records, together with records of actual numbers of cattle grazed, are used to compute regressions of the form:

$$S = b_1 A + b_2 P + a$$

where S is the number of cattle needed to utilize a given percentage (usually 40) of the perennial grass herbage, that is,

$$S = \frac{\text{Stocking} \times \text{utilization,}}{40}$$

A = annual grass production/acre,

P = perennial grass production/acre.

With these regressions we can estimate in October how many cattle are needed to utilize the given percentage of the perennial grass herbage by the following June. Annual adjustments in stocking based on these estimates have resulted in the desired degree of utilization on experimental pastures. Let us now consider what these records tell us about when, what, and how much the cows ate.

Suppose we wish to measure monthly forage consumption of 40 cows from vegetation measurements on an 800-acre unit on the Santa Rita Experimental Range. Average perennial grass herbage production is about 600 pounds per acre (90 percent is produced between July 1 and September 30); average utilization on June 30 is 40 percent. If each of the 40 cows consumes 20 pounds of dry matter per day, 24,000 pounds of dry matter is consumed each month. Since there are 800 acres in the unit, consumption per month of all species combined is 30 pounds per acre. We cannot estimate 30 pounds per acre of utilization (3.0 grams per 9.6-square-foot plot). However, since some plots may be grazed heavily and others not at all, we have a better chance to detect utilization than if all plots were grazed evenly. Thus, uneven grazing may be easier to detect but more difficult to quantify.

Some measure of the variability of forage production and use on range that produces 600 pounds of perennial grass per acre is indicated by the fact that standard deviations for individual species usually exceed the means (table 1). Herbage disappearance data (October 1 to June 30) derived from production and utilization estimates are even more variable than those for production. These estimates are based on 20 randomly selected permanent transects in an 800-acre pasture (1) where the mesquite has been removed and (2) where a fairly uniform grass cover has been established. Herbage yields on five permanent 9.6-square-foot plots at each transect are averaged to obtain the transect yield. The number of transects needed to sample within 20 percent of the mean at 90-percent probability ranges from 20 for total perennial grass herbage production to more than 1,300 for Rothrock grama. Disappearance estimates are products of herbage estimates after growth was completed and after utilization observations were taken in June at the end of the full year of grazing. The number of plots needed to estimate disappearance for a short period would be enormous.

TABLE 1.—*Production and disappearance (Lb/A) of perennial grass herbage and numbers of plots needed to sample within 20 percent of mean at 90 percent probability (Based on 1966 data from the Santa Rita Experimental Range)*

Species	Herbage				Transects needed (No.)		
	Production		Disappearance				
	Average	Standard Deviation	Average	Standard Deviation	Production	Disappearance	Utilization
Tall three-awn (*Aristida hamulosa* and *A. ternipes*)	85.6	135.5	31.0	52.5	170	194	34
Sprucetop grama (*Bouteloua chondrosoides*)	80.6	78.3	24.4	27.3	64	85	62
Slender grama (*B. filiformis*)	111.3	153.8	41.4	66.5	129	174	42
Rothrock grama (*B. rothrockii*)	6.2	28.0	2.8	12.3	1,380	1,308	680
Arizona cottontop (*Trichachne californica*)	35.0	61.4	22.3	42.7	308	248	73
All perennial grasses (include species not listed)	573.1	292.8	211.7	142.3	20	34	14

On the lower half of the Santa Rita Experimental Range, we graze about 50 cows on 5,000 acres. Again, if it is assumed that each cow consumes 20 pounds of dry matter per day, monthly consumption is 6 pounds per acre, or one-fifth as much as on better ranges. Obviously, average consumption per unit area under normal rates of stocking is too small to estimate for short periods with the present level of sampling.

INTERPRETING RESULTS

As a starting point, let us assume that a forage disappearance must be about 100 pounds per acre before we can measure it. Let us also assume that, with proper stocking, monthly consumption rates of 6 and 30 pounds per acre for low- and high-yielding pastures, respectively, are reasonable. Under these assumptions, we would have to stock the high-yielding range at more than 3 times the usual rate and the low-yielding range at 17 times the normal rate to produce measurable consumption in a month. Regardless of whether we measure animal response, forage output, or effects of grazing on vegetation, it will be difficult to derive practical management guides from results obtained by grazing at several times the intensity required for sustained forage production.

We can probably estimate the amount and composition of forage consumed by animals if certain conditions exist. Range units must be small enough, grazing intensities must be heavy enough, and grazing periods must be long enough to provide differences that are large enough to measure or estimate. Where forage production and rates of forage removal are relatively high, the paired-plot cage methods offer good possibilities for determining forage composition and consumption. Cage methods are especially useful during periods of rapid forage growth. Hand plucking the caged plot to match use on the open plot seems to have advantages over clipping both plots and determining consumption by difference.

On ranges of low productivity that are grazed at normal stocking rates, consumption during brief periods is too small to determine from vegetation measurements. Some clues as to the kinds of forage being taken can be obtained by checking favorite species and favorite areas, but quantities cannot be measured by methods in common use. General information on quantitative consumption can be accumulated by pooling data from several areas or several years, but the accuracy of such estimates is uncertain.

Forage consumed can be estimated by measuring the vegetation, by weighing the animal, or by observing what the animal eats. The strengths and weaknesses of estimates of forage consumption obtained from animals are adequately discussed by other contributors to this symposium. If the "vegetation" estimates differ from the "animal" estimates, which should we believe? Post-grazing vegetation measurements tell us very little about what a given animal ate on a given day. On the other hand, the activity of a given animal on a given day, or his weight change during a given period, tells us next to nothing about the impact of grazing on the range. Both kinds of measurements are necessary to properly evaluate vegetation-animal relationships.

CONCLUSIONS

Range science has developed several kinds of vegetation measurements that provide reliable guides for stocking the range. Such measurements can provide estimates of average forage consumption by livestock. For best results, sampling must be frequent and intensive, the rate of forage removal must be high, and unaccountable losses of forage must be low.

Grazing intensities on low-productivity ranges may have to be several times the level that is required for maintenance of the forage stand to produce a measurable effect on the vegetation in a short time. Consumption data so obtained may have little practical meaning.

Serious problems exist in recognizing the difference between (1) forage consumption by domestic livestock, (2) forage consumption by other animals, and (3) forage lost or displaced by physical forces of the environment.

Past forage use is not always visible. Invisible utilization may include plants that are pulled up by the roots, plant parts that are pulled out leaving no visible stubble, deciduous fruits or leaves, and use that has been obscured by subsequent growth.

Weathering and trampling can significantly reduce the amount of forage that is left at the end of the grazing period, thereby creating an impression either of low yield or high utilization, depending on the method of measurement used.

The use of cage methods provides estimates of growth during the grazing period and may reveal some invisible grazing. Cage methods have been satisfactory for pasture studies where production was high, grazing periods short, and consumption rather complete for each grazing period. Intensive range studies undoubtedly can use cage methods effectively.

Daily consumption of forage by animals varies with the quantity and quality of forage available, and with other factors that affect the metabolism—the energy budget—of the animal. Because of the many variables that influence animal performance, animal weight changes are not necessarily a good measure of forage consumption on the range.

Direct measurements of forage production and utilization reveal what is happening to the habitat generally, but they do not tell us what a given animal ate on a given day. Conversely, what one or several animals eat during a given period may tell us very little about the impact of grazing or browsing on the forage resource. Adequate information on range-animal relationships requires full use both of direct measurements of vegetation, and of measurements that employ animals as collectors or as collectors and processors of forage.

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Determining Forage Consumption by Direct Observation of Domestic Grazing Animals

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The purpose of this paper is to review methods of directly observing grazing animals—mainly cattle—to determine their forage consumption and possibly the reasons why they desire certain plants at certain times of the grazing season. The methods described are evaluated for research purposes.

Three basic methods are considered: (1) The cafeteria or free-choice method, (2) the feeding-minutes method and (3) the evaluation-of-grazing-patterns method.

GENERAL TECHNIQUES

One of the advantages of direct observation is that only a small investment in equipment is needed. Observations are conducted similarly in most cases; e.g., one or more men on foot watch selected animals. Binoculars are commonly used; however, observations have been done by the unaided eye. Sometimes a spotting scope is used to achieve greater accuracy. Flashlights and headlights have been used to aid night observation.

Brands, dyes, ear tags, and neck chains as well as natural coloring and conformation have been used to identify individual animals. Animals can be belled—a bell of different tone for each animal—to aid in locating them at night (Wagon 1963) and in the brush, or a radio tracking system can be used. However, the most common method to ease identification of individual animals is painting large numbers or letters on the sides of the test animals. Currie (1966) found that women's hair dye was an excellent marking liquid. Nelson and Furr (1966) added reflective glass beads to their marking liquid to aid in location and identification at night.

Some animals, especially sheep, are difficult to approach and must become accustomed to the observer. A blind, as suggested by Hughes and Reid (1951), can be used to hide the observer from the animals. Neal and Newman (unpublished 1968) used 15-foot portable hunting towers to increase visibility in shrub cover. Cattle become accustomed to the towers and graze very close to them. Cattle also allow close observation by men in a pickup truck (Reppter 1960) or by men on horseback, as they are accustomed to seeing men this way. When two or more men are observing, low-power citizen's band "walkie-talkie" radios are used to prevent duplication of effort—two men watching the same animal during the same period—or to assure duplication when it is desired. Radios used by two or more people also aid in locating specific animals without undue searching.

Sheep present a special problem because of their gregarious nature. The observer often loses sight of his subject in the band. It is difficult to observe grazing in the shrub communities because the larger plants restrict the view. Tame animals that can be followed closely are a great help.

Observation periods must be planned to coincide with the feeding periods of the animals, and the time pattern of feeding needs to be learned before the formal study is begun. Both sheep and cattle tend to do most of their feeding in the morning and evening. Cattle feed about 9 hours per day and sheep about 6.

Weather records are important when interpreting observation data and should be accurately kept during each observation period. For example, snowfall can force cattle to switch from grazing to browsing, and hot, humid conditions can cause them to graze in shaded areas.

As the observer works with a given vegetation type and class of animal, he gains skill rapidly. He learns to use animal position and movement, plant movement and even sounds to help determine what plant the animal is consuming. However, studies in California and Oregon have shown that even with experience and careful planning, it takes about 300 man-hours to observe animals for 100 hours.

Each method has certain advantages and disadvantages for research use. The methods are described here and are rated as range research techniques.

CAFETERIA OR FREE CHOICE METHOD

This method permits the animals to select their forage from a number of equally accessible species made available in approximately equal amounts (Joint Committee of the American Society of Range Management and the Agricultural Board 1962). The forage may be fed in bunks, in dry lot, or in pure-stand pasture plots. The animals feeding at bunks or plots

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containing a certain species are counted at specified times. Smith and Hubbard (1954) timed the animals as they fed at various stations and measured consumption by weight. Species were ranked in this method—those in certain bunks or on plots receiving the most use were considered more desirable. This system of ranking was also done by Cowlinshaw and Alder (1960). A replicated latin-square design using half-acre plots separated by isolation strips is desirable for plot work. Adequate replication should be provided. A factorial design including site and season of year as variables would provide information on site X plant species X season interactions.

The advantages of this method for use in research are: (1) Plant species can be easily ranked by the length of time animals spend on a plot and (2) all species are equally available. Disadvantages are: (1) The number of species to be compared is limited by the size of plot that can be practically and efficiently used and (2) the species must be grown in pure stands and the data must have questionable application for ranges with mixed-species composition.

This method has also been criticized because the rate of intake varies with animal fill and behavior may be disturbed by the presence of the observer (Hurd and Blaser 1962). It has also been criticized because the time spent grazing and the amount eaten may be poorly correlated; i.e., some foods are actively grazed and others are just nibbled (Jones 1952). However, Smith and Hubbard (1954), working with deer, found no significant difference between preference ranking of 15 browse species based on the time deer spent eating various species and the weight consumed.

FEEDING-MINUTES METHOD

The feeding-minutes method has been the most common method used to study feeding habits of livestock. The length of time spent grazing each species in a mixed stand is the index to preference and consumption. The observer must watch, with the aid of binoculars or a spotter scope, or at extremely close range, and time the animal as it bites off each plant. The contribution of each species to the diet is assumed to be proportional to the time spent grazing it.

The bite-count method is similar to the feeding-minutes method. Animals are observed while "free-grazing"; however, instead of recording the minutes spent grazing each species, the number of bites are recorded. Differential size bites is also a problem in this method. Different workers have used a wide variety of definitions of "bite"; several kinds of bite units have resulted. Sheppard (1921) reports a Hereford steer he followed gave 51 bites or "jaw wags" per mouthful while an Angus took only 30. This raises a question about the uniformity of the bites or the mouthfuls.

Reppert (1960) used a unit he called a "mouthful." This was the forage taken in from the time the animal lowered its head and began to graze until it stepped forward or stopped grazing in preparation to walking. Adjustments were made for the amount of forage consumed by recording one-fourth, one-half, three-fourths, or one mouthful. While somewhat subjective, this method probably does a better job of estimating relative consumption than either unadjusted bites or mouthfuls.

The sampling errors in the feeding-minutes or bite-count method can be similar to those associated with the cafeteria method; i.e., it is difficult to differentiate between active grazing and mere nibbling. Jones (1952) and Bjugstad and Dalrymple (1968) observed that animals would intensively graze some plants while only picking at others. Consequently, availability of plants would influence consumption (Herbel and Nelson 1966).

The feeding-minutes method plus hand plucking has been used not only to record species preference and a relative measure of consumption, but also to estimate nutrient intake. This method was described by Wagnon (1963) for California and by Bjugstad and Dalrymple (1968) for the Ozarks. They followed cattle while they were feeding and plucked hand samples of the same species and plant parts the cattle were taking. The samples were chemically analysed to determine the quality of diet. Halls (1954), using two people to closely observe cattle while grazing to determine diet, found good agreement among observers on species, but the amount of each species consumed was difficult to estimate. He also tried to estimate nutrient content of diet but concluded from chemical composition of plucked samples that a precise evaluation can be made only when special emphasis is placed on the selection of the plant portion actually being grazed.

EVALUATION OF GRAZING PATTERNS

This method is based on knowledge of grazing use on various range types in good condition at different seasons of the year. Deviations from established grazing-use patterns of range types indicate that desired plants are becoming scarce or deficient in nutrients and that more effort is being spent in searching for adequate forage.

The grazing-pattern method requires some background knowledge. Once this is available, grazing patterns can be used to determine when forage is inadequate, although quantitative data cannot be obtained by this method. The method has been employed in several areas in the United States—Ozark Region

(Bjugstad and Dalrymple 1968), prairie regions (Moorefield and Hopkins 1951; Weaver and Tomanek 1951; Hubbard 1952; Peterson and Woolfolk 1955; Dwyer 1961), the foothills of the Sierra Nevada (Wagnon 1963), and in Ceylon (Fernando and Sivalingam 1961) and in Japan (Nakata, Kaminaga, and Yokoyama 1962). These and other studies have contributed to the knowledge of established grazing patterns by providing observations of the changing seasonal grazing pattern due to plant selectiveness of grazing cattle. However, Hubbard (1952) observed that cattle showed no preference for different species, but would graze any species within reach before moving to another area. Also, Jones (1952) in Wales recognized grazing patterns but concluded that evening and morning dews altered the preference of stock for plant species to the point they desired and grazed certain areas over others. This points out the value of having microclimatic weather records when observing grazing animals.

The Bjugstad and Dalrymple (1968) study in the Ozarks showed that beef heifers grazed in old fields and open glades in mid-May where there was ample young, nutritious forage. But from late May to mid-July the grazing switched to open and closed woods, and the heifers searched for mushrooms even though the open areas still had plenty of forage. The protein and phosphorus content of grass and sedge forage was dropping to deficiency levels during this period. Apparently the cattle were alleviating a dietary deficiency by eating the mushrooms (high in protein and phosphorus) growing in the woods. But to do this, the animals spent much time searching and expending energy. Fernando and Sivalingam (1961) stated, "Energy expended in work, as a result of excess grazing, is used to the expense of production, particularly when herbage is sparse and supplementary feeding is not the general practice."

CONCLUSIONS AND SUMMARY

Direct observation of domestic livestock can determine *what* species and plant parts are being consumed, *when* (season) different species are eaten, *where* on the range the animals consume the forage, and *how* the animals feed. Observations alone, however, cannot determine *how much* forage is being consumed. The time and number of bites required to consume equal amounts of various types of forage are not necessarily equivalent. Observation methods do not determine the percentage of weight, height, or plants grazed. However, the ranking of relative preference is useful.

Observations on a mixed browse-grass range yield a ratio of all species eaten. Plant composition and density must be determined since availability may influence annual consumption. Herd composition must also be considered since a cow and calf herd may exhibit different preferences than a herd of steers.

Observations are made as animals feed. Observations are time consuming, especially on brushy ranges, and unfavorable weather can increase the time required to obtain adequate information. Plans must provide ample time, with leeway for unfavorable weather and other uncontrollable factors.

If there is sufficient need, interest, and time, then direct observations of livestock can yield good information on seasonal forage selected at different areas on the range. Direct observation does not give a good quantitative measure of consumption. However, this method can be used to measure deviations from established grazing patterns that can be useful to the range manager as an indication of forage inadequacies.

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Direct Observations of Tamed Deer to Measure Their Consumption of Natural Forage

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Knowledge of the preferences for and relative consumption of forages by wild animals is limited because of the difficulties imposed by their wildness. Several disadvantages are present in the methods that have been commonly used—stomach and feces collections, observation of wild animals feeding, measurement of use on the forage species, and offering of forages to animals kept in pens. To obtain information on forage preference and consumption, another approach, observation of tame animals feeding in the habitat of their wild counterparts, has recently been developed as a research technique.

This paper reviews the use of this technique with big game animals, and discusses problems in the acquisition and interpretation of data and methods of training and handling white-tailed deer and mule deer for such purposes.

HISTORY OF THE TECHNIQUE

Cory (1927) was perhaps the first researcher to obtain forage consumption data by closely following range livestock. Application of the direct observation method with livestock is discussed by Bjugstad et al. (see Bjugstad et. al. 1969 in this volume). With wildlife, of course, the obstacle is the disinclination of the animal to permit close observation. Several other workers [3] were all able to closely observe forage choices of tame or semitame deer or antelope. But not until 1959 was an effort made to employ specially trained wild or domestic ruminants in a systematic research plan as the principal measure of the kinds and amounts of forage taken on rangelands. This was done in Texas by McMahan (1964) with sheep, goats, cattle, and white-tailed deer in experimental pastures grazed at different intensities by these animals.

During 1962 and 1963, Watts (1964) used specially raised white-tails to determine forage consumption in relation to seasonal availability in hardwood forests in Pennsylvania. Healy (1967) continued this work in other areas in Pennsylvania. In connection with a multiple-use forest management research program in Arizona (Worley 1965), Wallmo (1964) and Neff (1966, 1967a, 1967b) raised and trained both white-tailed and mule deer to evaluate influences on diet of vegetation changes resulting from various land treatments. The only comparable foreign work known by the authors is that conducted with red deer by Dcieciolowski (1966) in Poland.

The advantage of using an approachable tame animal to determine forages taken on wild lands can be summarized in a statement by Dunkeson (1955) who had one very tame white-tail and one intractable captive: "Close observation of this deer made possible discovery of food preferences and use of forage which normally goes unseen. The other deer was too elusive to be observed on the brushy terrain."

The other conspicuous advantage is the control the scientist can exercise over his sampling procedure. He, rather than chance, determines the times and places from which data are acquired. Yet, if random times and places are a desirable feature of an experiment, they also can be introduced at the discretion of the investigator.

COMPARABILITY OF TAME AND WILD ANIMALS

Subjecting a wild animal to the confinement necessary to tame it inevitably alters its behavior and its experience with food. This has been a principal objection to the use of such animals for forage preference and utilization studies. For this reason, Wallmo (1951) did not initially use the tame antelope available when he was attempting to observe the feeding of wild antelope. They had been nursed on cow's milk and raised on hay, grain, tobacco, candy, and garbage. However, after observing them grazing with wild antelope for several days, it was apparent that they were distinguishable only by the tags in their ears, not by their behavior or forage choices.

Likewise, Buechner (1950) concluded, "The semitame antelope instinctively selected the same principal plants in the same proportions as the wild animals. . ." McMahan (1964) said, ". . .observations were made on wild deer feeding in the same area as the tame animal. These comparative observations gave the impression that the gentle deer's grazing habits were not different from those of wild deer. Both the tame deer and the wild animals appeared to eat the same browse and weed species." Healy (1967) felt that ". . .the captive deer behaved in the same manner and exhibited forage preferences similar to those of wild deer."

While it can be speculated that prior nutri-

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[3] Lindzey (1943), Hahn (1945), Buechner (1950), Wallmo (1951), Dunkeson (1955), and Brown (1961).

tional status and familiarity with forages might influence choices in a given situation, Neff (1967b) said, "The food choices of Wallmo's pine country deer from Flagstaff when taken to an enclosure in the chaparral near Prescott in 1964, were almost identical to those I had observed in local deer."

The prevailing evidence, mostly empirical, indicates that captive animals exhibit preferences for natural forage similar to those of wild animals. McMahan (1964) even concluded that the level and timing of supplementary feeding caused little difference in the deer's grazing behavior. Watts (1964) concurred: "Initially the deer were not fed for 24 hours prior to field observation, but this practice was later discontinued because it appeared to have no effect upon feeding time of the deer in the field."

What animals eat is greatly determined by inherent characteristics of their digestive physiology (see Nagy 1969 in this volume). Longhurst et al. (1968) contend that the sensing and selection of acceptable foods by deer involves smell, touch, and taste. It may be assumed that any native forage that is sensed as palatable by a tame animal will be acceptable to a wild animal, and vice versa, barring marked differences in the prior nutritional status of the animals. This becomes most problematical when tame animals, maintained on an adequate pen ration, are grazed where wild animals are finding forage supplies inadequate. However, it might shed light on the true palatability of species being taken by wild animals under such conditions.

SIGNIFICANCE OF INDIVIDUAL VARIATION

In biological research it is accepted that attributes of an individual may differ widely from the mean of a population. The hazards of basing conclusions on the effects of or effects on too few individual animals are well known in range and livestock husbandry research. In comparing the forage choices of two each of sheep, goats, cows, and deer, McMahan (1961) found that ". . . no two individuals of each class (except the two cows) were from the same statistical population . . ." It was Healy's (1967) opinion that "Future studies . . . should incorporate additional deer to determine the significance of individual variation in feeding habits. Because only three deer were used, it is impossible to assign preference weights to deer by sex."

Probably each study requires either pretesting to determine the number of animals needed to acquire data of desired quality or, on the basis of existing limitations, using arbitrary numbers and kinds of animals and accepting the inherent limitations in the results.

FORAGE IDENTIFICATION

The opportunity to identify any and all forages consumed is a most attractive aspect of direct observation of tame animals. Forages of unknown taxonomic identity can be collected or marked for future identification. Occasionally the items eaten are so small that they cannot be seen from a normal observing stance. In such cases the authors have gone to hands and knees and even snatched fragments from the deer's mouth to see what is being taken.

Parts of plants chosen and their phenological state can be noted. Equally important, species or plant parts that are consistently ignored or are tested and rejected by the animal can be noted.

QUANTIFICATION PROBLEMS

The reported studies by direct observation have used either time spent feeding[4] or number of bites[5] to measure the relative use of different forages.

Healy (1967) specified that the time measurement began with biting off or picking up the forage item, included chewing, and terminated with swallowing. Where the bite is the unit of measure, apparently most workers have considered it the act of breaking off or of picking up a piece of forage. This piece might consist of one part or several parts (several stems or leaves in one bite).

According to Smith and Hubbard (1954), ". . . quantity of material consumed from the various species cannot be accurately estimated by observation of feeding-minutes, for deer consume forage from different species with varying degrees of efficiency." The same might be said of bite counts. A better approximation should result if the feeding time or bites can be expressed in terms of weight of forage consumed. Neff (1967b) has proposed that weight per bite be determined by plucking "bites" by hand from each species of forage plant soon after the completion of deer-feeding observations at each sample site. The average dry weight of 20 to 40 simulated bites would be used to estimate the weight of material consumed by the deer: the number of real bites x mean weight of simulated bites = amount consumed.

Frels and Veteto (1966) attempted to determine mean weights of portions of plants taken by a deer and a cow, and to record the exact portions of each bite taken. They have recently found this approach to be unworkable, and are now evaluating forage intake using esophageal cannulae (personal communication).

[4] Hahn 1945; Buechner 1950; Watts 1964; Healy 1967.

[5] Wallmo 1951; Brown 1961; McMahan 1964; Dzieciolowski 1967; Neff 1967b.

When relative quantities consumed are used as an index to relative preference for different kinds of forage, it usually is understood that intake is influenced both by availability and palatability. In developing preference ratings from data on forage use by tame deer, Watts (1964) include percent species composition of the total available vegetation on belt transects:

$$\text{Preference} = \frac{\text{Total feeding} - \text{seconds}}{\text{Percent availability}}$$

Neff (1967b) proposed the following procedure:

$$\text{Preference} = \frac{\text{Number of bites} \times \text{mean weight per bite}}{\text{Estimated availability}}$$

in which mean weight per bite was determined from plucked samples, and species were ranked in visually estimated abundance classes. In determining relative preferences of different classes of animals for the same forage species within the same pastures, McMahan used differences between classes in the mean number of bites of that species.

Relative preference is obviously a complex abstraction which is not completely resolved by these methods.

TRAINING AND HANDLING

The first step in taming and training is to teach the animal to rely on the human trainer. This is best done by bottle feeding a new-born animal which has been separated from the dam. This involves much work and the probability of digestive upsets, but an acceptable level of tameness is the natural result of several weeks of frequent feedings. There seems to be no difference in tameness between wild-caught and pen-born deer fawns when both are handled and fed the same way.

Observation of pen-raised, tame, trained deer at Flagstaff shows that even the most tractable individuals retain some inherent wildness. They all are startled, even panicked, by loud noises or sudden movements. They are easily frightened if they begin to feel crowded or if they are caught and held for more than a few seconds. Fundamental to a successful training program is the avoidance of all frights and stresses which the deer might associate with the training procedures. A young horse may respond well to gentle but unyielding force in training, but this approach would probably cause chronic blind panic if applied to deer. At Flagstaff we have occasionally had to tackle the deer for medication, but such manhandling is to be avoided as much as possible.

Training deer is greatly facilitated by the use of pens and other equipment designed for a quiet, uneventful operation. Of course, all equipment is designed to avoid injury to deer. The whole operation must also be escape proof. The operations of harnessing and unharnessing, and loading and unloading from the truck, must all be accomplished quickly and without exciting or restraining the deer. A favored food may be used as bait to keep the deer interested during harnessing and to entice the animal into the pen or vehicle. However, deer currently being used by the Rocky Mountain Forest and Range Experiment Station are so gentle they permit harnessing even when they are lying down.

Training for harness work has been described by Watts (1964), Healy (1967), and Neff (1967b), and for free-ranging work by Wallmo (1964). Essentially, the training consisted of frequent handling and petting, harnessing and leading, feeding in the vehicle, and short rides. The most careful and consistent training program may be unsuccessful with some individuals. Two of five mule deer doe fawns captured on the North Kaibab in 1965 refused to accept harnessing and were never used in the field (Neff 1967b). However, both McMahan (1964) and Wallmo (1964) were able to train deer to feed in the field and to reenter the vehicle without any kind of physical restraint.

With harnessed deer, the observer can lead the animal away from sample area boundaries or from dangerous objects such as cliffs and fences, and lead them back to the pen or vehicle after feeding trials. Although the deer are permitted as much free rein as possible during trials, this leading capability gives the observer full control when he needs it. If the harness is not used, it is necessary to establish in the deer complete reliance in its handler. This security bond ensures that the deer will not stray off for long. We have learned in current work in Colorado that some deer that do not accept being led still can be used effectively without a harness.

A holding pen on or near the sample area is highly desirable, and an adequate transport system is vital. Watts (1964) and Healy (1967) each used a trailer for transport. Wallmo (1964) and Neff (1966) were faced with numerous, separate sampling areas connected by rough roads poorly suited to trailer hauling. The final solution was a utility-bed pickup truck with a custom-built enclosed deer compartment and a removable loading ramp. Frels and Veteto (1966) used a standard pickup bed with a woven wire enclosure and an integral loading ramp.

The time of day and length of observation period has varied with the handling methods and research objectives. McMahan (1964) used 45-minute periods, 1 period per day, and 4 days per week. Several observers used 1 to 2 hours per trial period (Watts 1964; Neff

1967b) while others devoted most of the day to the job (Brown 1961; Healy 1968) (Marchinton and Baker [6]) The governing factors were the behavior of the deer and the length of time they spent actively feeding, as well as the particular research needs.

Where the research objectives call for semitame animals which are approachable in a large enclosure or on open range, special training is required. Marchinton and Baker [6] achieved this with a white-tailed buck fawn by initial bottle feeding followed by a period of minimal human contact and isolation from other deer, first in a box stall and then in a 1.6-acre pen. This deer developed as an approachable but independent animal well suited for food-habits observations of free-ranging deer.

Dunkeson (1955) combined free movement, approachability, and control over sampling area by releasing a pet deer in a 90-acre enclosure. Dcieciolowski (1966) observed his tame red deer hind in an enclosure including various forest conditions and permanent water. Where such enclosures exist or can be built in a suitable habitat, handling is minimal and training may consist only of bottle feeding until the animal is weaned. However, the cost of fencing sample areas of adequate size will often be prohibitive. Use of movable paddocks (Smith and Gaufin 1950) provides one solution to this problem.

The ultimate achievement in close observation of big game animals without interference might be that of Graf (1955), who was able by frequent contacts to condition wild Roosevelt elk to his presence at close range. This program was carried out in an Oregon State park where the elk had never been hunted. Brown (1961) observed black-tailed deer that had been raised by hand but that had been allowed to roam free most of their lives. These animals were essentially wild in habits, but still approachable. Marchinton and Baker [6] located their deer in the woods daily by radio-tracking procedures. Such methods permit close observation without frequent manipulation, but leave the choice of study area entirely up to the animals.

There is no apparent reason why elk, moose, or other big game animals should not be tamed and trained for studies of food habits and for other studies. Bison have been successfully trained as draft animals; however, they are somewhat untrustworthy (Garretson 1938). The use of reindeer as saddle, pack, and draft animals is well known (Zhigunov 1968). Tamed Aoudad sheep, sika deer, and axis deer are being used in Texas in the evaluation of food habits of exotic ungulates (Ramsey 1968). With larger animals, however, much greater caution in handling will be necessary than has been the case with deer.

EXPERIMENTAL CONTROL

The paramount advantage of using tractable wild animals for observing forage intake is that observations can be planned in relation to specific interests—vegetation types, pasture treatments, seasons, etc. McMahan's (1964) work is the outstanding example of the applicability of the technique in a complex experimental design. On the Kerr Wildlife Management Area (Texas Parks and Wildlife Department), a series of ten 96-acre pastures was used to study how different intensities of grazing by cattle, sheep, goats, and deer affected deer production. Pronounced differences in response of deer were obtained (McMahan and Ramsey 1965), but measurements of vegetation or of utilization did not explain the relationship of diets of various classes of animals to grazing treatments. To obtain this relationship, McMahan used tame animals of each class, grazing them daily for a year, according to a time-and-place design through four seasons in four pastures, which represented the range of conditions existing in the 10 experimental pastures. He used a factorial analysis of variance, the pertinent variables being animals, pastures, and seasons, to determine *between* and *within* differences in amounts taken of species and classes of forage in all combinations. From these analyses, he was able to define the nature of interspecific competition in pastures and seasons, and to conclude that the variety and abundance of forbs was the principal factor influencing the performance of deer.

Watts (1964) obtained clip-and-weight samples of total available forage in six arbitrary seasons, and graphically compared relative availability with relative use on a 4-acre area of hardwood forest in Pennsylvania.

Work currently being conducted by the second author, Neff, is concerned with the effect of various kinds of vegetation manipulations on the welfare of game populations. To determine the effect of treatments on the forage supplies of deer, treatments are applied and controls are retained, the response of understory vegetation is measured, and the feeding of tame animals is observed.

SUMMARY

Numerous researchers have used tame or semitame pronghorn antelope, red deer, white-tailed deer, or mule deer to study forage consumption by these species. In a few cases, such

[6] Marchinton, R. L., and Baker, M. F. Direct observation & feeding behavior of radio instrumented deer. Unpublished personal communication, 1968.

animals have been employed in experiments to determine the effect of different vegetation types and seasons, grazing treatments, or range manipulations on kinds and quantities of forage taken. The resulting experience demonstrates that some wildlife species can be trained and handled for effective use in forage studies related to specific research objectives.

The salient advantages are: Opportunity for positive identification of all foods taken; recognition of species, parts, or phenological stages of plants that are unacceptable as forage; ability to relate selections and rejections to availability in a desired time and place; opportunity for sampling in conformance with predesigned plans and even to incorporate the forage consumption measurements in an experimental design without additional cost for fencing or facilities in the experiment itself. An outstanding advantage is the large quantity of data that can be acquired relative to other methods.

However, the technique has not yet been fully perfected. There is not yet a satisfactory method of quantifying intake. Methods for demonstrating or establishing an acceptable degree of similarity between tame and wild animals are not available. Variability between individual animals and the requirements for obtaining data relevant to a population are poorly known. The time, effort, and cost of acquiring, rearing, and training the animals are imposing.

In employing a research technique, the important consideration is how well it answers the question being asked. If it is what *kinds* of forage are being consumed by the subject animal or animals, this method works very well. If it is the *amounts* consumed, the method is so far crude. If it is to determine the kinds and amounts of forage consumed by populations of such animals, much work has yet to be done to establish its reliability.

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Chemical Indicator Techniques for Determining Range Forage Consumption [1]

BRENT THEURER [2]

The problem of measuring forage consumption on native range is both important and difficult. The system devised by Garrigus and Rusk (1939) is often used in estimating forage consumption of the grazing animal: calculation of dry matter consumption is based on the feces collected during the test period. This procedure involves determining the digestibility of the forage and measuring fecal excretion. With these parameters, dry matter consumption may be computed from the formula:

$$\text{Dry matter intake (kg.)} = \frac{\text{Fecal excretion (kg.)}}{100 - \%\ \text{dry matter digestibility}} \times 100$$

The determination of range forage consumption by chemical indicator techniques is an indirect method which depends upon the reliability of the indicators to accurately estimate digestibility and fecal output.

The determination of the digestibility of grazed forage depends on a knowledge of the composition of both the fecal material and the ingested forage. Using a naturally occurring indicator in the forage, digestibility may be determined indirectly by the fecal-index method or by the indicator-ratio technique. Fecal excretion may be determined by total fecal collection or by the use of external indicators. Reviews on the use of indicator methods for determining consumption and digestibility of forage by grazing animals have been prepared by Harris et al. (1959), Weir et al. (1959), and Bohman and Lesperance (1967).

DETERMINATION OF DIGESTIBILITY WITH INTERNAL INDICATORS

The fecal index technique is based on the relation of some fecal chemical constituent to digestible organic or to digestible dry matter. With this method, the internal indicator does not need to be indigestible, and is measured only in the feces after representative dietary samples have been fed to determine the index relationships. This technique may be used if the forage is relatively uniform, and it is palatable when it is hand clipped and fed. Since much range forage is not only heterogeneous but also unpalatable when hand fed, the indicator-ratio techniques appear more promising for estimating digestibility. The ratio technique involves the use of a naturally occurring substance in the forage, and determination of this indicator in forage and feces. The relation is as follows:

$$\text{Digestibility (\%)} = 100 - 100 \times \left\{\frac{\%\ \text{indicator in forage}}{\%\ \text{indicator in feces}} \times \frac{\%\ \text{nutrient in forage}}{\%\ \text{nutrient in feces}}\right\}$$

Collection of Forage Samples

The validity of the ratio technique depends upon collection of forage samples representative of the animal's diet and of a representative sampling of fecal material. Since grazing animals exhibit considerable selectivity, forage ingested by the animal differs in composition from herbage available (Weir and Torell 1959; Lesperance et al. 1960b; Galt et al. 1966). The inability of investigators to hand sample forages representative of that ingested by livestock has led to the use of fistulated animals to collect naturally grazed samples. For this purpose Torell (1954) devised an esophageal fistula. A collection bag with a screen bottom is attached to the animal's neck, and the animal is allowed to graze until a sufficient sample has been obtained (Van Dyne and Torell 1964). Lesperance et al. (1960a) developed a technique to utilize rumen-fistulated animals as forage samplers. The rumen and reticulum are emptied thoroughly prior to releasing the animals to select forage samples.

McCann et al. (1967) [3] noted that both dry-matter intake and fecal output were significantly greater for intact than for rumen fistulated steers grazing a summer grassland range in northern Arizona (table 1). Average weight gains during the summer grazing period were also somewhat greater for the intact steers. The estimated digestibility of dry matter, gross energy, and crude protein of forage grazed were not different between fistulated and intact steers. Rumen evacuations were conducted at the time of the final fecal collection and therefore did not influence digestibility; however, the rumen evacuations, fistulation *per se*, or both markedly influenced dry matter intake. This is an agreement with hand-feeding trials using the same steers (McCann and Theurer 1967). These data suggest that the use of rumen-fistulated steers to estimate forage intake,

[1] Arizona Agricultural Experiment Station Technical Paper 1380.

[2] Associate Professor, Department of Animal Science, University of Arizona, Tucson, Ariz.

[3] McCann, C. P., Theurer, B., and Pearson, H. A. 1967. Unpublished data. University of Arizona, Tucson, Arizona and Rocky Mountain Forest and Range Experiment Station, Flagstaff, Arizona.

as well as for forage sampling, would underestimate the intake of intact steers of comparable size and condition.

TABLE 1.—*Comparison of fistulated and intact steers grazing range forage*[1]

Steer treatment	Digestibility			Average daily—		
	Dry matter	Gross energy	Crude protein	Dry-intake matter	Fecal output [2]	Gain
	Percent	Percent	Percent	kg.	kg.	kg.
Fistulated	35	36	48	[3] 3.4	[3] 2.2	0.47
Intact	35	36	48	[4] 5.0	[4] 3.3	.60

[1] See footnote 4, p. 111. There were four steers/treatment and five observations/steer during a 97-day study period.

[2] Dry-matter basis.

[3,4] Means in same column with unlike superscripts differ significantly ($P<.05$).

Ridley et al. (1963) reported that digestibilities were similar for rumen-fistulated and intact cattle. This report is in contrast to their Nevada studies (Lesperance and Bohman 1963; Connor et al. 1963). In these latter three studies, rumen contents for fistula forage sampling were removed on 3 different days during the digestion trials. Rumen-fistulated animals may be used for digestibility studies if the rumen evacuations for forage sampling are not conducted during the digestion study. In many range studies, it would be advantageous to obtain several forage samples during simultaneous digestion and intake studies. In these studies, rumen-fistulated animals should be used only for forage sampling, and a second group of intact animals should be used to estimate forage intake and digestibility.

Indicator Comparisons Based on the Ratio Technique

Various substances have been utilized in an attempt to predict digestibility by indirect methods; these substances include silica, methoxyl, lignin, chromogens, crude fiber, and protein or nitrogen. Because of analytical difficulties, stratification in the gastrointestinal tract, variable natural occurrence in the feed, or partial absorption, some of these substances either have been eliminated from consideration as indicators or have not been investigated sufficiently to establish their potential value. The indicator most commonly used for estimating digestibility of range forages has been lignin; however chromogens and silica have been used.

Cook and Harris (1951) compared chromogens and lignin as indicators for sheep grazing on winter desert range. The coefficient of variation averaged 8 to 12 percent for lignin and 20 to 21 percent for chromogen with sheep grazing two types of shrubs. They concluded that under these conditions chromogens were unreliable as indicators. These workers also reported that dry-matter digestibility of alfalfa hay is similarly estimated by the chromogen and lignin ratio techniques. Interactions between indicator and type of forage may be important. Bohman et al. (1967) cite studies conducted at the University of Oregon in which low recovery of chromogen pigments was obtained with hand-fed steers. These studies are not in agreement with those of Connor et al. (1963), who found chromogen to be more suitable than lignin for estimating dry-matter digestibility on range forage.

Jefferies and Rice (1967) compared the lignin and chromogen ratio techniques for estimating digestibility of a native shortgrass range for steers. Digestibility estimates varied significantly between techniques and between sampling periods. Estimates by the two methods did not follow the same trend throughout the summer. The modified chromogen technique gave much higher digestibility estimates for dry matter. More studies are needed to clarify the validity of chromogens to estimate digestibility for grazing livestock under range conditions.

Van Dyne and Lofgreen (1964) evaluated lignin and silica as digestibility indicators of forage grazed by cattle and sheep on summer annual range. The three grazing periods varied in the relationship of the digestion coefficients calculated by the two indicators. Digestion coefficients calculated by silica ratio varied widely during the summer grazing periods. Their data suggest that silica can accumulate temporarily within the animal's digestive tract, and may cause biased digestibility values when used as an inert indicator.

Lignin Ratio Technique

Three problems have been associated with the use of lignin as an indicator: (1) Development of a simplified, repeatable technique for measurement of the indicator in forage and fecal samples; (2) obtaining forage samples with lignin content representative of that consumed by the animal; and (3) constant, repeatable recovery in the fecal material.

Van Soest (1964) critically reviewed the procedures used for lignin analyses. He concluded that proteinaceous material, hemicellulose, and products of nonenzymatic browning reaction were artifacts generally present in the lignin fraction isolated by many of the common procedures. Van Soest (1963) showed that proteins and hemicellulose which were interfering could be effectively removed by treatment of the forage with an acid detergent solution. His studies indicated that the nonenzymatic browning reaction could be largely prevented by maintaining the drying temperature below 50°

C. Due to the relative simplicity and repeatability of the acid detergent lignin method, it has been used in most of the more recent reports citing the lignin ratio technique.

Early studies (Bath et al. 1956; Lesperance et al. 1960a) indicated that salivary contamination significantly modified the composition of fistula forage samples by increasing the ash content. Other studies have indicated differences in chemical composition of fistula samples as compared to hand-clipped or hand-fed forages (Connor et al. 1963; Hoehne et al. 1967). In the studies by Hoehne et al. (1967), no change was observed in the acid detergent lignin content of squeezed or nonsqueezed esophageal samples as compared to samples of two hand-clipped grass species. However, soluble carbohydrate fractions were lower in the fistula samples. In contrast, Lesperance et al. (1960a) and Ridley et al. (1963) reported that rumen samples from animals which were evacuated prior to grazing were higher in lignin contents than hand-harvested forage samples. Connor et al. (1963) reported that the concentration of lignin was higher in rumen fistula forage samples than in various hay and pasture feeds.

McCann et al. (1967)[4] noted wide differences between the acid detergent lignin content of available range herbage and rumen fistula forage (table 2). Lignin content in these fistula samples averaged 68 percent higher than the average lignin content in the four major grass species available. In every instance, the indicator content of the fistula forage samples was greater than that of any single grass sample analyzed. Some of the differences noted between the herbage and fistula forage samples may be due to selective grazing. However, similar discrepancies in lignin content of rumen fistula and hand-fed forage samples have been reported by McCann and Theurer (1967) and by Lesperance et al. (1967).

Lesperance and Bohman (1964) reported that the addition of water or of artificial saliva to hay samples, followed by drying, increased acid detergent lignin and decreased nitrogen-free extract as compared with the original hay samples. Similar results were also observed when rumen fistula forage samples were compared to original hay samples. Their studies also indicated that drying temperature had a significant influence on lignin and carbohydrate composition of the various samples.The lignin content of oven-dried (65° C.) samples was significantly greater than that of samples vacuum-dried at 25° C. or frozen and lyophilized. In later studies, Smith et al. (1967) found that lignin was significantly higher in oven-dried (65° C.) samples of rumen fistula forage or feces as compared to freeze-dried samples, while nitrogen-free extract was significantly lower. Ash content was significantly higher in all types of oven-dried samples. Absolute dry matter percentage was lower, suggesting the possible loss of dry matter during oven drying.

These studies suggest that the higher lignin content of rumen fistula forage as compared to original forage may be an artifact largely attributable to sample preparation. Absorption of soluble carbohydrate in the rumen during forage collection by the grazing animal may also contribute to this problem.

Lesperance et al. (1967) reported that dry-matter digestibility estimated by the lignin-ratio technique was altered by the drying method used for fistula forage and fecal samples. Estimates of intake and digestible dry matter based on oven-dried samples did not differ significantly from actual values, but were significantly overestimated with freeze-dried samples. Van Dyne and Lofgreen (1964) reported no significant difference in digestion coefficients calculated by the lignin ratio when forage and fecal composition were on a dry matter basis, silica free or organic matter basis; this indicates that ash from salivary contamination of esophageal fistula forage samples had no significant influence on the estimation of digestion coefficients. The apparent differences in acid detergent lignin content of hand-fed versus fistula forage has been primarily associated with forage obtained from rumen rather than esophageal-fistulated animals. Further studies are needed to clarify chemical changes in fistula samples, as well as the effect of sample preparation on the use of lignin as an internal indicator for estimating digestibility.

Determining percent recovery of acid detergent lignin from animals consuming range forage in many instances is not feasible. Harvesting of range forage for conventional digestion studies is not often possible because of the heterogeneous nature or scarcity of the herbage. Apparent digestibility of acid detergent lignin by cattle fed alfalfa hay has been determined in studies conducted at the Arizona

[4] See footnote 4, p. 111.

TABLE 2.—*Percent acid detergent lignin in forage samples collected by hand clipping and rumen fistula* [1,2]

Sample collection	Period 1	2	3	4	5	Average
Hand clipped [3]	5.1	4.8	4.4	4.7	4.7	4.7
Rumen fistula [4]	8.6	7.6	7.5	8.2	7.8	7.9

[1] See footnote 4, p. 111.
[2] Dry-matter basis.
[3] Average lignin content in the four major grass species available on a ponderosa pine range in northern Arizona during the 1967 grazing season. Values for individual species varied from 4.0 to 6.1 percent lignin.
[4] Average of samples obtained from four steers.

station (table 3). Acid detergent lignin was not completely recovered in any of the studies reported. Apparent digestibility of acid detergent lignin in alfalfa hay was approximately 10 percent; however, average values in various trials ranged from about 7 to 13 percent. In the studies of McCann and Theurer (1967), apparent digestibility of acid-detergent lignin ranged from −3 to 17 percent for individual steers fed alfalfa hay in two trials.

TABLE 3.—*Apparent percent digestibility of acid detergent lignin by cattle fed alfalfa hay*

Investigator	Number of Animals	Number of Observations	Apparent digestibility
Trei & Hale (1965)[1]	4	24	7.6
Amavisca (1966)[2]	8	12	12.6
Lambeth (1966)[2]	12	12	11.3
McCann and Theurer (1967)	8	16	12.0
Loynachan (1968)[2]	12	12	6.8
Total or average	44	76	10.1

[1] Trei, J. E., and Hale, W. H., 1965, Unpublished data on file at Univ. Ariz., Tucson, Ariz.
[2] Unpublished M.S. Thesis, Univ. Ariz., Tucson, Ariz.

Lesperance et al. (1967) reported apparent digestion coefficients for acid detergent lignin of −45 ±25 percent and −29 ±18 percent in studies with steers fed freshly cut grass. It is not clear whether these large negative values were associated with the type of forage or with some factor unique in this study. Using the 72-percent sulfuric acid method of Ellis et al. (1946) for lignin determination, other workers have noted incomplete recovery of lignin of from 1 to 24 percent (Kane et al. 1950; Balch 1957; and Elam and Davis 1961). Incomplete recovery of lignin will bias nutrient digestibility values downward. More studies are needed to determine recovery of acid detergent lignin from animals with several forage species varying in moisture content. An accurate estimate of lignin recovery is necessary to obtain meaningful digestibility coefficients with the lignin-ratio technique. Although complete recovery of lignin is desirable, it is not necessary since appropriate correction factors may be effectively used (Lucas 1952) if percent recovery can be adequately determined.

McCann and Theurer (1967) compared dry-matter digestibility estimated by acid-detergent lignin with actual values obtained from steers fed alfalfa hay (table 4). Dry-matter digestibility values obtained by the lignin-ratio technique using total fecal collection or single daily fecal grab samples were similar but differed significantly ($P < .05$) from actual digestibility determined by total collection. This difference was due to the incomplete recovery (88 percent) of lignin in the fecal samples. Average percent of fecal lignin did not differ between grab samples and total collection samples, but day-to-day fecal lignin concentration was significantly different ($P < .05$). McCann (1967)[5] estimated that four steers and 3 days were required to estimate dry-matter digestibility using the lignin-ratio technique with a 95-percent confidence interval of ±10 units of the mean with a probability of 95 percent. Van Dyne and Lofgreen (1964) estimated that three animals (sheep or cattle) were required to estimate dry-matter digestibility within 10 percent of the mean with 90 percent confidence; the average numbers of forage plus fecal animals (sheep or cattle) required to estimate digestion coefficients for crude protein, ether extract, other carbohydrates, or cellulose were 29, 25, 6, and 5.

TABLE 4.—*Estimated percent dry-matter digestibility determined by lignin-ratio technique*[1]

Trial	Steers	Total collection	Lignin-ratio technique: Total feces samples	Lignin-ratio technique: Fecal grab samples[2]
1	8	[3] 58.4	[4] 53.8	[4] 52.8
2	8	[3] 62.8	[4] 56.6	[4] 57.1
Average	--	[3] 60.6	[4] 55.2	[4] 55.0

[1] McCann and Theurer (1967).
[2] Once daily at 7:00 a.m.
[3,4] Means on same line with unlike superscripts differ significantly ($P<0.05$).

ESTIMATION OF FECAL EXCRETION AND FORAGE INTAKE

Fecal output from grazing animals can be measured directly by means of harness and collection bags (Garrigus and Rusk 1939), but this equipment may influence grazing behavior, cause the animal considerable distress, and increase the energy expenditure. Loss of fecal material from collection bags may be excessive if the bags are not carefully adjusted for each animal and if the bags are not emptied frequently (often two or three times daily). The animal must be thoroughly accustomed to the collection apparatus if the intake data obtained is to be meaningful. The results of Hill et al. (1961) indicated that feces production may be overstimulated when collection bags are used intermittently for 4-, 6-, or 24-hour collections. Meyer et al. (1956) found that the average daily gain of steers fitted with a fecal-collection harness was significantly less than for those without a harness. It was suggested

[5] McCann, C. P. 1967. Nutritional studies using chromic oxide and lignin ratio techniques with rumen fistulated versus intact steers. Unpublished M.S. Thesis, University of Arizona, Tucson, Arizona.

that the difference could have been attributed to decreased consumption by the harnessed steers.

Because of the difficulties associated with total fecal collection coupled with the brushy nature of many native ranges, many investigators have utilized an external indicator to estimate fecal output. Fecal excretion is determined from the relationship of indicator administered to that excreted:

$$\text{Fecal dry matter output (gm)} = \frac{\text{gm. Indicator administered}}{\text{gm. Indicator/gm. fecal dry matter}}$$

The disadvantage of this method is that the animals must be assembled one or more times daily so the indicator can be administered and fecal grab samples can be collected. Accurate estimation of fecal output by use of an external indicator depends upon a constant or a 100-percent recovery of the material in the feces. Chromic oxide (Cr_2O_3) has been the most frequently used external indicator.

Chromic Oxide Recovery as Influenced by Method of Administration

Chromic oxide has been administered in various forms and at different intervals to reduce variability in fecal excretion of the indicator. Considerable diurnal variation has been reported with the use of chromic oxide powder, whether mixed with the ration (Kane et al. 1952) or administered in gelatin capsules (Hardison and Reid 1953; Pigden and Brisson 1957; Raymond and Minson 1955). Irregularities in feeding pattern and animal behavior enhance irregularities in excretion by cattle and sheep (Balch et al. 1957). Fecal concentration of chromic oxide has been shown to be more variable in grazing than in hand-fed animals (Hardison and Reid 1953; Raymond and Minson 1955).

Administration of chromic oxide powder in gelatin capsules and collection of fecal grab samples at the same time twice daily has been successfully employed with cattle grazing forage (Lesperance and Bohman 1963; Connor et al. 1963). These workers found that fecal excretion values were essentially the same whether determined by grab samples or total collection. Other workers have noted considerable variability in the use of chromic oxide powder under range conditions (Bohman et al. 1967).

Corbett et al. (1958) reported that incorporation of chromic oxide in paper gave more uniform flow of the indicator through the duodenum of sheep than administration of chromic oxide powder in gelatin capsules. Later studies (Corbett et al. 1960) indicated that administration of chromic oxide in shredded paper significantly reduced the variability of fecal excretion in sheep as compared to the powdered form given in an oil suspension. In similar comparisons with both cattle and sheep, Cowlishaw and Alder (1963) and Langlands et al. (1963) reported less variation in fecal concentration with the shredded-paper technique.

Bohman et al. (1967) reported on studies conducted at the Oregon station in which the variation in fecal chromic oxide recovery was reduced by mixing the indicator with cellulose. In three trials conducted with steers grazing native range, recovery from total collection samples averaged about 100 percent, with a range of from 88 to 112 percent, when the cellulose mix was administered twice daily in gelatin capsules. When fecal grab samples were taken twice daily at the time of dosing, the estimated fecal output averaged about 99 percent of actual dry-matter excretion.

Chromic oxide administration and collection of grab samples at less frequent intervals would be extremely advantageous under most range conditions. McCann (1967) [6] found that administration of a chromic oxide-cellulose mixture once daily resulted in rather constant excretion of chromic oxide from the fourth to twelfth day of administration from steers hand-fed alfalfa hay (table 5). Daily recovery, expressed as a percent of the mean for each 9-day study, ranged from 94 to 110 percent and from 94 to 108 percent in trials 1 and 2, respectively. Day-to-day variations in fecal excretion were not significant. These studies agree with similar data reported by Green et al. (1966) for chromic oxide paper administered once daily.

Use of Chromic Oxide in Paper or Cellulose Mixtures.—Various studies in which chromic oxide paper or chromic oxide-cellulose mixtures have been given to cattle or sheep are

[6] See footnote 5 p. 114.

TABLE 5.—*Daily recovery of chromic oxide expressed as percent of mean recovery.*[1, 2]

Day[3]	Trial 1[4]	Trial 2[4]	Average
4	102.1	106.9	104.5
5	99.8	98.1	98.9
6	96.6	107.7	102.2
7	95.7	103.8	99.8
8	98.9	96.6	97.8
9	100.7	98.6	99.6
10	94.4	94.0	94.2
11	110.0	95.7	102.8
12	101.6	98.3	100.0

[1] See footnote 5, p. 114.
[2] Chromic oxide mixed in a 1:2 ratio with cellulose and administered once daily in gelatin capsules.
[3] Days after initial administration of indicator.
[4] Average of eight steers per trial.

summarized in table 6. Corbett et al. (1960) found that 4 to 6 days were required for excretion of chromic oxide in feces to equilibrate with intake of chromic oxide administered in shredded paper once daily. Similar observations have been made in more recent studies on chromic oxide paper (Green et al. 1966) and chromic oxide-cellulose mixtures (McCann and Theurer 1967).

Since fecal output (percent of actual) is

TABLE 6.—*Percent recovery of chromic oxide administered in shredded paper or on cellulose*

Indicator form, feeding method, and forage type	Number and kind of animal	Time of dose Cr_2O_3 A.M.	Time of dose Cr_2O_3 P.M.	Time of grab sample A.M.	Time of grab sample P.M.	Days to equilibrate	Percent recovery [1,2] Total collection	Percent recovery [1,2] Grab sample	Investigator
Shredded Paper:									
Hand fed:									
Grass hay	4 sheep	10:00	------	------	------	4–6	98.6	----	Corbett et al. (1960)
Do	4 sheep	10:00	------	10:30	4:30	---	101.8	102.3	do.
Do	6 steers	6:00	------	6:30	------	3	96.8	93.2	Green et al. (1966)
Do	6 steers	6:00 (every other day)	------	7:00	------	4	97.6	113.1	do.
Do	3 steers	twice daily	twice daily	------	------	---	100.1	----	Streeter (1966) [5]
Freshly cut grass.	3 steers	do.	do.	------	------	---	99.5	----	do.
Grazing:									
Pasture	3 sheep	8:00	4:00	8:40	4:40	---	97.9	100.9	Langlands et al. (1963)
Do	3 sheep	8:00	------	8:40	------	---	99.7	105.8	do.
		8:00	------	------	4:40	---	----	72.2	
		8:00	------	8:40	4:40	---	----	89.8	
Pasture + hay.	3 steers	9:00	4:30	9:00	4:30	---	94.2	98.9	do.
Pasture	2 steers	9:00	------	[3] Continuous	[3] Continuous	----	94.4	[3] 93.0	Cowlishaw & Alder (1963)
Native range (2 trials).	6 steers	6:00	6:00	[3] Continuous	[3] Continuous	---	90.6	[3] 83.1	Streeter (1966) [5]
Native range (3 trials).	5 heifers	5:00	5:00	------	------	---	89.6	----	do.
Cellulose Mixture [4]									
Hand fed:									
Alfalfa hay (2 trials).	8 steers	7:00	------	7:30	------	4	81.8	95.8	McCann & Theurer (1967)
Meadow hay	2 steers	twice daily	twice daily	8:00	4:00	---	----	81.0	Bohman et al. (1967)
Grazing:									
Native range (2 trials)	12 steers	do.	do.	twice daily	twice daily	---	99.8	97.0	do.
Native range + supplement (3 trials)	16 steers	do.	do.	do.	do.	---	100.7	103.8	do.
Native range.	4 steers	7:00	------	7:30	------	---	76.2	80.5	Galt et al. (1968) [6]

[1] Adapted from investigator's data where not given directly.
[2] Based on fecal concentration and on concentration necessary for complete recovery; or on reciprocal of estimated fecal output.
[3] Refers to composite collection of fecal "pats" from the ground.
[4] Chromic oxide powder was mixed with Solka Floc (The Brown Co., Berlin, N.H.).
[5] Unpublished Ph.D. Dissertation, University of Nebr., Lincoln, Nebr.
[6] Unpublished data. University of Ariz. and Rocky Mountain Forest & Range Exp. Sta., Tucson, Ariz.; see footnote 11, p 117, Galt, H. D., Theurer, B., and Martin, S. C. 1968.

equal to the reciprocal of indicator recovery most of the studies cited (table 6) would overestimate fecal excretion and thus forage intake. Chromic oxide recovery in total fecal collections ranged from 90 to 102 percent for paper administration. Estimated recovery from grab samples varied from 72 to 113 percent. The lack of information on the use of chromic oxide paper and grab sampling techniques with livestock grazing native range is apparent.

Fewer studies have been reported on the use of chromic oxide-cellulose mixtures (table 6); however, animal numbers approach those in studies with chromic acid paper. Most of the cellulose mixture trials were conducted under range conditions, with single or twice-daily grab sampling. Recovery values ranged from 76 to 101 percent for total collection samples and from 80 to 104 percent for grab samples.

The low recovery values noted in these studies are difficult to explain. Incomplete recoveries with chromic oxide powder have been noted by several workers (Crampton and Lloyd 1951; Clanton 1962; Johnson et al. 1964). Retention or absorption of chromic oxide powder in the digestive tract appears to be of minor importance (Carter et al. 1960). Small fecal losses in the total collection methods are to be expected and probably account for some apparently low recoveries. The magnitude of this error with the use of collection bags in studies with animals grazing range forage is difficult to determine. Partial recovery of the chromic oxide in the fecal material does not limit the usefulness of the indicator for estimating fecal output, since appropriate adjustments can be made if the percent recovery is constant.

Regurgitation of gelatin capsules containing chromic oxide paper or cellulose mixtures has been noted by several workers (Corbett et al. 1960; Streeter 1966;[7] McCann 1967)[8]. The "sustained release pellet," which is composed of chromic oxide and plaster of Paris (Pigden and Brisson 1957), has not been satisfactory with sheep due to regurgitation (Corbett et al. 1960). Streeter (1966)[7] placed capsules containing chromic oxide paper directly into the esophageal fistula of steers to alleviate this problem. Green et al. (1966) did not note regurgitation of shredded paper containing chromic oxide that was wrapped in paper and was given orally without capsules. Howard (1965)[9] placed chromic oxide cellulose mixtures (wrapped in filter paper) directly into the rumen of fistulated steers.

Fecal excretion of chromic oxide apparently is altered by feeding condition (hand fed vs. grazing) as well as by time of fecal grab sampling and indicator administration (table 6). Langlands et al. (1963), using chromic oxide paper once daily, obtained recoveries of 106, 72, and 90 percent with grazing sheep as measured by morning, evening, and combined morning and evening grab samples. The mean standard deviation of the difference between fecal collection and estimated fecal output from the morning grab samples was ± 24 percent, as compared to the corresponding value of ± 13 percent obtained from both morning and evening samples.

Arizona workers (McCann and Theurer 1967) found grab sampling once daily (7:30 a.m.) at the time of administration of a chromic oxide-cellulose mixture satisfactorily estimated fecal output from steers fed alfalfa hay under controlled conditions (table 7). Under range conditions, this same technique overestimated fecal excretion by 24 percent (Galt et al. 1968).[10] The studies of Green et al. (1966) showed that fecal output of cattle would be underestimated by 12 percent using every-other-day grab sampling with concomitant administration of chromic oxide paper. Their studies were conducted under confined conditions and may not be applicable under range conditions.

Corbett et al. (1966), using shredded chromic oxide paper, suggested that 14 grab samples from sheep (twice daily per animal), would estimate chromic oxide concentration within a standard error of ± 3 percent. McCann (1967)[11] administered a chromic oxide-cellu-

[7] Streeter, C. L. 1966. Methods of estimating the digestibility and voluntary intake of range forage consumed by grazing cattle. Unpublished Ph.D. Dissertation on file at University of Nebraska, Lincoln, Nebr.

[8] See footnote 5, page 114.

[9] Howard, M. L. 1965. Unpublished data on file at University of Arizona, Tucson, Ariz.

[10] Galt, H. D., Theurer B., and Martin, S. C. 1968. Unpublished data. University of Arizona and Rocky Mountain Forest and Range Experiment Station, Tucson, Arizona.

[11] See footnote 5, page 114.

TABLE 7—*Estimated fecal output from chromic oxide concentration in single daily fecal grab samples* [1 2]

Trial	Forage	Steers	Actual output [3]	Estimated output: Output	Estimated output: Percent of actual output
		Number	*Gm./day*	*Gm./day* [3]	
1	Hay, hand fed	8	2,148	2,413	111.4
2	Do.	8	3,168	3,196	99.7
3	Native range	4	2,926	3,634	124.2

[1] McCann and Theurer (1967). See footnote 11, above (Galt et al. 1968).

[2] Chromic oxide mixed in a 1:2 ratio with cellulose and administered once daily.

[3] Dry matter basis.

lose mixture to cattle once daily and calculated that four animals and 12 days were required, with single daily grab samples, to obtain a 95 percent confidence interval of ± 10 units of the recovery mean with a probability of 95 percent. Van Dyne and Meyer (1964) determined that the average number of animals required to estimate forage intake from a dry annual range using lignin ratio and total fecal collection methods would be 4 and 22 sheep or 2 and 6 cattle to sample forage and feces, respectively.

SUMMARY

Use of chemical indicators to measure forage consumption indirectly, by estimating digestibility and fecal excretion, presents unique problems under range conditions. Lignin has been the primary internal indicator used to estimate digestibility of range forages, and chromic oxide is the most common external indicator for measurement of fecal output.

Hand sampling of forage representative of that ingested by a grazing animal is not possible because of pronounced grazing selectivity from the heterogeneous, seasonally changing plant composition available on native rangeland. The use of esophageal- or rumen-fistulated animals is the best method for sampling the grazing animal's diet. Fistulation *per se* does not appear to affect forage digestibility. However, evacuation of rumen-fistulated cattle to obtain forage samples during the digestion study may lower digestibility values. It should also be recognized that if rumen-fistulated animals are used to measure fecal output, forage-consumption values will be biased downward compared to nonfistulated animals of similar age and weight.

Preparation of fistula forage samples for chemical analyses is a critical step because the method of drying appears to alter certain fractions, notably lignin. The increased concentration of lignin in rumen fistula forage samples relative to conventional forage samples markedly limits the usefulness of the lignin ratio technique until causative factors can be quantified and refinements can be made to correct the inflated lignin values. Acid detergent lignin has an apparent digestibility in alfalfa hay of approximately 10 percent. The recovery of acid detergent lignin from other plant species is not known and needs to be determined to permit measurement of the digestibility of range forage.

Erratic recovery of chromic oxide in fecal grab samples and loss of the indicator by regurgitation of gelatin capsules have been the major problems limiting the use of chromic oxide under grazing conditions. Incomplete recovery of the indicator does not invalidate the technique if percent recovery is constant and can be reasonably quantified. The introduction of chromic oxide in shredded paper and chromic oxide-cellulose mixtures has markedly reduced variation in fecal excretion of the indicator under grazing conditions. Administration of chromic oxide paper in paper boluses may minimize losses due to regurgitation.

Although refinement of the indicator methods is needed, recent research has clarified the variables so that meaningful forage consumption values appear possible with these techniques.

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Water Intake by Cattle as a Measure of Forage Intake and Quality

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INTRODUCTION

Semiarid grazing lands present numerous obstacles to adaptations of agronomic and nutritional methods to range research. Such lands are characterized by large acreages of natural vegetation, limited production of forage, ecological variability in species composition, species sensitive to herbage removal, great variations in the quantity and quality of forage eaten by grazing animals, and striking seasonal changes in diet composition. We must, of course, obtain the greatest possible advantage from the research methods that require artificial restrictions on land and animals. Also, we must have research methods that can be used without restricting land and animals. Economic limitations require a rather extensive type of land and animal husbandry in which ecological relations can seldom be replaced by cultural practices. Consider, for example, the quantity and quality of forage eaten by grazing animals. Large pastures of natural vegetation generally offer a great variety of species and conditions from which the animals select food and cover that is favorable, or at least pleasing, to them. Thus, ecological interactions cannot be ignored, and experimental results from greatly restricted situations can be unrealistic. So, one must have research methods that can be used to determine the important factors and interactions of plants, animals, and soils on semiarid grazing lands without excessive restriction.

This need prompted our interest in the water-dry matter intake dependency of cattle as defined by Winchester and Morris (1956); and our interest in the net energy equation as applied by Lofgreen (1963) and coworkers. Progress in our research is summarized in this paper. Three topics are involved: (a) The water-intake method of estimating forage intake by grazing cattle; (b) the adaptation of the net-energy equation for estimating forage quality; and (c) the use of water-soluble tracers for estimating water use and partitioning.

THE WATER-INTAKE METHOD

Initial Development

Derivation.—Our work began in 1964 with an interest in the possibilities of using the water-intake rates of cattle to estimate forage intake by grazing cattle. Winchester and Morris (1956) gave water-intake rates (in gallons of water consumed per pound of food dry matter eaten) as a function of ambient temperature. Since their work was based on a substantial number of data, the water-dry matter intake relations should be valid for a variety of conditions. The original data can be equated in the form:

$$H = KF, \tag{1}$$

where H represents the total amount of water consumed (in gal), K represents the water-intake rate (in gallons of water per pound of dry matter consumed at any given mean air temperature in degrees F.), and F represents forage intake (in pounds of dry matter eaten per head daily. By solving for F, we obtained the desired expression:

$$F = H \div K. \tag{2}$$

Equation 2, however, must be expanded to include as separate components the water in forage and the water taken by drinking. A table of forage-intake rates (in pounds of dry matter eaten per gallon of water drunk for any given set of mean air temperature in degrees F. and percentage of moisture content of forage) was computed. Thus, a solution for forage intake was given as the product of the amount of water drunk and the forage-intake rate (Hyder et al. 1966a). The method requires the measurement of water drunk, mean air temperature, and the percentage of moisture in the forage. These measurements are nonrestrictive. Drinking water is measured by metering, air temperatures are recorded by a thermograph, and moisture contents of forage are estimated from hand-plucked samples of herbage collected while moving with and observing the selectivity of the grazing animals.

Initial Testing.—The water-intake method was compared to the agronomic method of clipping before and after grazing in 1965. This experiment was arranged to facilitate the estimation of forage intake by the clipping method, even though such an arrangement was a disadvantage in applying the water-intake method. Grazing by yearling Hereford steers was restricted to areas of about 1 acre for 3 days at biweekly intervals for a total of six trials in the summer of 1965. The mean forage intake was estimated to be 23.3 and 22.8 pounds of dry matter per head per day by clipping and water-intake methods, respectively. Since true forage intake is unknown, the reliability of the two methods must be judged on a statistical and intuitive basis. Two separate factors allow intuitive evaluations: one is animal size in

[1] Range Scientist, Crops Research Div., ARS, USDA, Ft. Collins, Colo.

paired observations, and the other is seasonal changes. In each of six trials spaced at 2-week intervals through the season, the steers were grouped into uniform liveweight classes called small and large.

The forage-intake equation is as follows (Hyder et al. 1966a):

Let: K = the water-intake rate in gallons of water per pound of dry matter consumed by European breeds of cattle at any given degree F. mean air temperature (Winchester and Morris 1956).

H = total water intake in gallons per day.

H_d = the gallons of water drunk.

H_f = the water content of forage in gallons per pound of dry matter = (% water ÷ % dry matter) ÷ 8.345 lb./gal.

F = forage intake in pounds of dry matter per day.

F_r = the forage-intake rate in pounds of dry matter per gallon of water drunk.

Thus:

$$H = KF \qquad (1)$$

$$F = H \div K \qquad (2)$$

Substituting:

$$F = (H_d + FH_f) \div K \qquad (3)$$

Solving for F:

$$FK = H_d + FH_f$$

$$FK - FH_f = H_d$$

$$F(K - H_f) = H_d$$

$$F_r = H_d \div (K - H_f) \qquad (4)$$

Let $H_d = 1.0$ gal:

$$F_r = 1.0 \div (K - H_f) \qquad (5)$$

Forage-intake rates (F_r) were calculated for various combinations of mean air temperature °F.) and moisture contents of forage (%). Thus, the final solution for forage intake (F) is given by:

$$F = F_r \times H_d \qquad (6)$$

Application to lactating animals is accomplished by subtracting the water content of milk from H_d.

Trial 2 also included a medium-size class. In table 1 the results obtained are grouped by size classes and trials. The authors (Hyder et al. 1966a) believe that forage intake by size classes and trials (for seasonal changes) was estimated in a more consistent and reasonable way by the water-intake method than by the clipping method. Even with this restriction in area and duration of grazing, the clipping method is rated as only slightly successful. Its weakness was surely due to the small standing crops, which imposed an extremely high requirement in sampling precision. As we shall see from results of subsequent research, the restrictions upon area, grazing duration, and number of animals made the water-intake method disadvantageous.

TABLE 1.—*Forage intake as estimated by water-intake and herbage-clipping methods in 1965*

Trial	Mean-live-weight, by size class: Small	Large	Forage intake, by method and size class: Herbage clipping: Small	Large	Water intake: Small	Large
	Lb.	*Lb.*	*(Lb./head/day)*	*(Lb./head/day)*	*(Lb./head/day)*	*(Lb./head/day)*
1	515	646	36.0	27.4	26.3	29.2
2	545	691	16.8	22.1	20.6	26.2
3	641	719	28.1	28.8	25.3	25.1
4	610	752	16.4	20.0	17.0	22.2
5	652	755	15.8	14.8	13.8	20.1
6	679	787	25.0	18.6	15.3	22.2
Mean	607	725	23.0	22.0	19.7	24.2

Adjusted Forage Intake.—Since we desire to reveal the effects of changing pasture conditions on forage intake, the estimates obtained should be adjusted to compensate for the differences and seasonal increases in yearling liveweight. We chose to make this adjustment according to the function of animal metabolic size. Thus, the adjusted forage intake (F_{adj}) was that proportional part of the observed forage intake prorated to a yearling metabolic size ($W^{.75}$) of 100 (see equation (8); Hyder et al. 1966a). With animal size discounted, the variability among estimates indicates sampling precision. However, sampling precision among the estimates of adjusted forage intake is more exactly defined by the residual variance after removing the seasonal effect among trials. In this way, the mean adjusted forage intake and standard deviation are estimated to be 17.5 ±4.0 and 16.9 ±1.6 pounds per day by clipping and water intake, respectively. (Note: These calculations were made without including the data for the medium-size class of trial 2.) Although sampling precision can be irrelevant to sampling accuracy, it is nevertheless highly important in comparing methods.

Sampling Requirements

Methods.—The encouraging results obtained in 1965 prompted a more intensive experiment in 1966—one planned to fulfill the objective of defining the sampling requirements and inherent limitations of the water-intake method (Hyder et al. 1968a). Twelve yearling Hereford steers were allowed to graze a half-section, blue-grama pasture continuously from May 17 to October 5, 1966. The first 2 weeks were reserved for preconditioning and training of steers. Metered drinking water was provided in individual pens to which the steers

were admitted daily from about 11 a.m. to 4 p.m. Records of water drunk were omitted for days when rainwater was ponded on the pasture. Air temperatures were recorded continuously by thermograph. Hand-plucked samples of herbage were collected while moving with and observing the selectivity by the steers each morning and evening 3 days each week. The data obtained were used to estimate forage intake for each 2-week period, and to determine the sampling requirements of each type of measurement.

Forage intake.—The mean adjusted forage intake varied from 16.1 to 25.4 lb./day, with 5 percent confidence limits based on differences among steers varying from ±1.1 to ±3.5 lb./day. Increases and decreases in forage intake among periods coincided with increases and decreases in the moisture content of forage (table 2). The relation of forage intake to moisture content of forage has been defined more completely elsewhere (Hyder 1967). Forage intake probably was overestimated in grazing periods 2, 6, 7, and 8 (1966), when the steers ate much Russian thistle (*Salsola kali* L.) as well as blue grama (*Bouteloua gracilis* (HBK) Lag. ex Steud.). There is no reason to suspect a bias in the estimate of forage intake when the moisture content of forage was less than 60 percent.

TABLE 2.—*Adjusted forage intake and moisture content of forage in 1966*

Grazing period	Adjusted forage intake	Moisture content of forage
	Pounds/day	*Percent*
1. 5/31–6/14	16.7	48
2. 6/14–6/28	25.4	71
3. 6/28–7/12	17.8	58
4. 7/12–7/26	17.5	49
5. 7/26–8/9	17.2	51
6. 8/9–8/23	23.5	69
7. 8/23–9/6	24.1	70
8. 9/6–9/20	24.8	68
9. 9/20–10/4	16.1	56

Amounts of water drunk.—Mean water-dry matter intake relations are presumed not to apply to a single animal for any time interval, or to a single day for any number of animals. In other words, the proper application of mean water-dry matter intake relations requires an appropriate sample size stated with respect to number of animals and number of days. Individual animal-day observations are needed for the computation of variance components and sample structure. Since we cannot readily obtain under pasturing conditions the ratios of water to dry matter consumed, this analysis is based on the amounts of water drunk. As estimated from the separate components of variance for differences among steers and for differences among consecutive days within a week, a sample should include: 11 head over 14 days, 15 head over 7 days, or 16 head over 4 days.

Mean air temperature.—Mean air temperatures derived from daily minimum and maximum values were compared with means derived from temperatures recorded at 3-hour intervals. Weekly means expressed to the nearest degree F. were nearly always identical by the two procedures, and never differed by more than one degree. Therefore, the simple procedure of averaging minimum and maximum daily temperatures is retained.

Moisture contents of forage.—Weeks and time of day were sources of highly significant differences in the moisture contents of hand-plucked herbage. The residual mean square provides an evaluation of sampling precision that may be used to estimate the number of samples needed in a 2-week grazing period. Under the conditions encountered in 1966, 31 samples would have been appropriate. Thus, when only 12 samples are taken in each grazing period, this characteristic was under-sampled. The difficulty one encounters in hand-plucking to estimate the mean moisture content of forage consumed can vary from slight to extreme, increasing with an increase in the moisture content of forage. The kinds of variability encountered require a systematic daily (morning and evening) observation and collection of herbage. Although one develops confidence in this procedure, the accuracy attained in duplicating the animal diet cannot be determined in absolute value.

Inherent Limitations

High temperatures.—A limitation is inherent in the basic relations defined by Winchester and Morris (1956). High temperatures increase the requirement for water in the control of body temperature, and decrease the relative importance of the dry-matter function. Thus, the amount and variability in the amount of water required per pound of dry matter consumed increased with increased temperature. This variability becomes excessive at constant temperatures greater than 90 F., but our highest 14-day mean temperature is about 75 F.

High moisture contents of forage.—Theoretically the complete water requirement of cattle can be supplied by the water contained in the forage (Hyder et al. 1966a). In that event, the amount of water drunk theoretically would be zero, and forage intake could not be estimated. As the moisture content of forage increases, the relative importance of drinking water decreases. The limiting effect of high-moisture forage can be shown by calculating the errors in forage intake that would result from an error in estimating the moisture content of forage. Take, for example, an error of just +2 percent in estimating the moisture content of

forage (table 3). The resulting error in forage intake increases with an increase in true moisture content of forage. When the moisture content exceeds 65 percent, the magnitude of error (associated with a high probability of occurrence) becomes unbearably large. This is a limiting factor because we cannot attain infinite precision and accuracy in sampling this characteristic.

TABLE 3.—*Percentage of error in forage intake estimates resulting from an error of +2 percent in the estimate of mean moisture content of forage*

True moisture content of forage, percentage	Mean air temperature (°F.), percentage of error in forage intake estimates				
	40	50	60	70	80
20	1.4	1.1	0.8	0.5	0.6
30	1.9	1.7	1.2	1.0	1.1
40	2.3	2.2	1.9	1.8	1.1
50	4.3	3.6	3.0	2.5	2.0
55	6.3	5.3	4.3	3.5	2.9
60	9.0	7.9	6.1	4.6	4.0
65	16.4	13.3	9.6	7.2	5.2
70	44.4	30.5	18.8	12.3	8.6

Sources of Bias

Factors affecting vapor output.—Increasing temperatures increase the requirement for water in the control of body temperature. Thus, ambient temperature was evaluated by Winchester and Morris (1956) as the primary factor in the water-intake rates of cattle. They reviewed literature showing that the effect of humidity was negligible below 75 F. Wind, also, is most likely to become important only at high temperatures, when respiratory and cutaneous excretion of water is great (Brody et al. 1954). The literature apparently does not include data on the effects of radiant heat independent of air temperature. However, it has been shown that shades of insulating materials are beneficial to cattle in hot weather (Ittner et al. 1954). Several environmental factors can affect the water-intake rate, especially when temperatures exceed 90 F. The high variability in water-intake rates at high temperatures probably is due to the effects of variations in wind, humidity, and radiant heat as well as to a magnification of inherent animal variability. Although these environmental factors seem unlikely causes of bias in estimating forage intake under our field conditions, consideration of them leads to the assumption that: if one could determine the amounts of water excreted through the skin and lungs, and express the water to dry matter relation in terms of the water requirement for urine and feces, then the usefulness of the water-intake method could be improved and extended to a wider range of conditions.

Factors affecting liquid output.—According to the literature reviewed by Winchester and Morris (1956), the intake of large amounts of nitrogen and salt increases the water requirement. Water intake by sheep increased 3.4 liters per 100 grams of increase in salt intake (Wilson 1966a). Forage containing high concentrations of salt increased the water intake and decreased the dry matter intake (Wilson 1966b). Most of the salt (89 to 98 percent) is excreted in urine (Riggs et al. 1953; Wilson 1966b). Excess waste products from nitrogen metabolism, as well as salt excess, must increase water output in urine, and thereby increase the water-intake rate. With crude-protein contents of forage varying from about 18 percent in the spring to about 5 percent in the fall, we must expect some seasonal pattern of bias in estimating forage intake. Generally, high crude-protein contents of forage are associated with high moisture contents, which we have suspected had a positive bias in the estimate of forage intake. In all probability, we need an adjustment based on the nitrogen content of forage.

Variations in the water content of feces also must be considered. Russian thistle appears to have a laxative effect, which might result from its high oxalate content (Cave et al. 1936; Christensen et al. 1948). We found an increase in the moisture content of feces of as much as 4 percent when yearling steers were eating a large proportion of Russian thistle. This factor alone increased water output in feces about 1 gallon per day, and surely must have caused a positive bias of 3 to 5 pounds in the estimate of forage intake. Consequently, we anticipate the need for an adjustment based on the water content of feces.

Synopsis.—Our greatest difficulties are associated with high moisture contents of forage. Inherent limitations, inadequate sampling precision, and potential sources of bias have been encountered simultaneously with high moisture contents. Adjustment procedures that will permit an extension of usefulness for the water-intake method surely can be developed without losing the advantages of low cost, ease of application, and lack of requirements for restricting animals and land area. Meanwhile, opportunities to improve the efficiency of grazing practices on semiarid grasslands are most likely to coincide with low moisture contents of forage (Hyder 1967). Needless to say, we like the water-intake method, even though we must express a very strong desire to improve it and extend its usefulness (for estimating forage intake and quality, pasture productivity, and herbage growth rates as discussed by Bement)[2] to a wider range of pasturing conditions.

[2] Bement, R. E. 1968. Herbage growth rate and forage quality on shortgrass range. Ph.D. Thesis on file at Colo. State Univ., Fort Collins, Colo., June 1968, 53 pp.

NET ENERGY

Adapting the Net Energy Equation

The net energy equation, as formulated by Winchester and Hendricks (1953), was adapted to pasture conditions by the addition of a travel (walking) component for which the energy coefficient was adopted from Brody (1945). Coefficients for maintenance and gain were adopted from the results of Garrett et al. (1959). Thus, when animal liveweight, gain, and travel are known, the total amount of net energy (NE_{m+p}) received daily from pasture can be estimated by solution of the net-energy equation:

$$NE_{m+p} = 38W^{.75}\ (1+0.45G) + 0.33\ WT, \qquad (7)$$

where W represents animal liveweight in pounds, G represents animal daily gain in pounds, and T represents the distance traveled in miles.

Prorating this total amount of net energy received to a unit weight of forage dry matter was accomplished according to the theory of separate values for maintenance and production proposed by Lofgreen (1963). We chose to express forage quality to a value for maintenance at zero production (Hyder et al. 1966b). This procedure, of course, has no connection to water intake, except through the use of the water-intake method of estimating forage intake. Since the net-energy equation is not expected to apply specifically to a single animal over any given period of time, the problem of sample size is equivalent to that encountered with respect to water-intake rates.

Forage Quality

Forage quality can be evaluated and quantified (in part) in several ways, such as by dry-matter digestibility, organic-matter digestibility, total digestible nutrients, digestible energy, metabolizable energy, starch equivalents, and net energy. The net-energy value is most definitive but indicates animal as well as forage characteristics. However, dry-matter digestibility is least definitive but most limited to forage characteristics. In the practical sense, forage value (as opposed to "quality") can be expressed in terms of the efficiency of forage conversion to beef. which is a function of forage intake as well as quality. For example, normal (that is, modal) forage conditions on blue grama range for yearling Hereford steers are defined by the following results (Hyder 1967):

Normal forage conditions

Forage conversion rate	=	10.5 lb./lb.
Steer daily gain	=	2.2 lb./day
Forage intake	=	23.2 lb./day
Adjusted forage intake	=	19.0 lb./day
Net energy value of forage	=	690 kcal./lb.
Crude protein content of forage	=	12.7 percent
Amount of herbage standing	=	400 lb./acre

Inefficient forage conversion rates were encountered in May, when the adjusted forage intake was only 14.2 lb./day and the net energy value was only 410 kcal./lb., and in October, when the adjusted forage intake was less than 14 lb./day and the net energy value was greater than 600 kcal./lb. In May, forage intake was limited by the small amount of herbage standing (120 lb./a.), but in October it was limited apparently by low moisture (less than 50 percent) and low crude protein (less than 8 percent) contents of forage. Beef production per acre could be increased an estimated 40 percent by omitting inefficient pasturing conditions. However, economic advantage would also depend on the cost and efficiency of alternate practice.

Sampling Problems

The use of the net-energy equation to estimate the apparent net-energy quality of forage requires the measurement of forage intake, animal liveweight, daily gain, and daily travel. Sampling requirements have not been evaluated in detail, but the critical and sensitive parts of the calculations have become obvious —these are animal daily gain and forage intake. Yearling Hereford steers have a daily water turnover of about 80 pounds. Weather and forage conditions sometimes induce changes in liveweight of greater than 30 pounds in a single day. Yet, we need to measure daily gains over short intervals, at least biweekly, to properly associate animal performance with existing herbage conditions. The point of view is that the animals determine forage intake and quality, and these two factors can then be interpreted for the development of more efficient grazing practices. When we devote a considerable expenditure of time and money in our research programs to livestock, and have within our grasp the ultimate manifestation of forage value, the deficiency of measurement techniques and of fundamental data about animal-forage relations is intolerable. Since animal daily gain is essential to this approach, we must find a way to measure it. The prospect is not entirely dismal. Difficulties in measuring daily gain appear to arise primarily from variations in the amount of water contained in the animal, although we cannot disregard variability in the dry-matter content of the gut. Liveweight is composed of up to about 70 percent water, and cattle appear to have a water turnover rate that is two to three times greater than that of other ruminants (Macfarlane 1965). Morris et al. (1962) reported that the total body water content of sheep varied from 50 to 67 percent of liveweight. Animal liveweights presumably should be adjusted to a constant total-body-water percentage. Research methods applicable to this

problem involve the injection and subsequent dilution of water-soluble markers (Black et al. 1964; Budtz-Olsen et al. 1961; Hydén 1961; Macfarlane et al. 1966; Till and Downes 1962; Ulyatt 1964a; and others). We also need to consider physical and electrical phenomena such as beta particle attenuation and electrical capacitance for detecting body water contents.

DRINKING-WATER TRACERS

Suitable drinking-water tracers can supplement or replace dry-matter tracers for the estimation of fecal output, forage intake, and digestibility. Beyond these functional applications, water tracers can be used to obtain more fundamental information concerning water turnover and partitioning by animals in grazing environments. Three water tracers are needed to determine water turnover and partitioning by nonlactating animals. One tracer should move throughout the animal system and should be excreted in all water vapor and liquid phases. The other two tracers should equilibrate and be excreted separately in urine and feces to permit the calculation of the individual water components. When the respective volumes of water are known, then dry matter, nutrient, and mineral concentrations therein can be expanded to total quantities.

Deuterium oxide, lithium chloride, and erythrosine have been tested at the Central Plains Experimental Range as potentially valuable drinking-water tracers equivalent to markers A, B, and C of figure 1, respectively (Hyder et al. 1968b). Since the results of this research are included in a manuscript that is in review for publication, they cannot be given here. However, it is appropriate to say that we experienced more problems than success. The erythrosine disappeared completely, and the determinations for deuterium led to some ridiculous estimates. Lithium, on the other hand, was recovered almost entirely in the urine (95 to 99 percent) (see also Ulyatt 1964b). Since the amount of water drunk was metered to the steers, the change in lithium concentration from drinking water to urine provided an estimate of the amount of water excreted in urine.

Other appropriate water tracers should be investigated. Analytical and sampling problems should be solved, because drinking-water tracers surely can provide new methods of determining animal-forage relations on a herd or lot basis without imposing severe restrictions on land, animals, or grazing practices.

SCHEME OF WATER TURNOVER AND PARTITIONING WITH THEORETICAL PATHWAYS FOR WATER TRACERS A, B, AND C

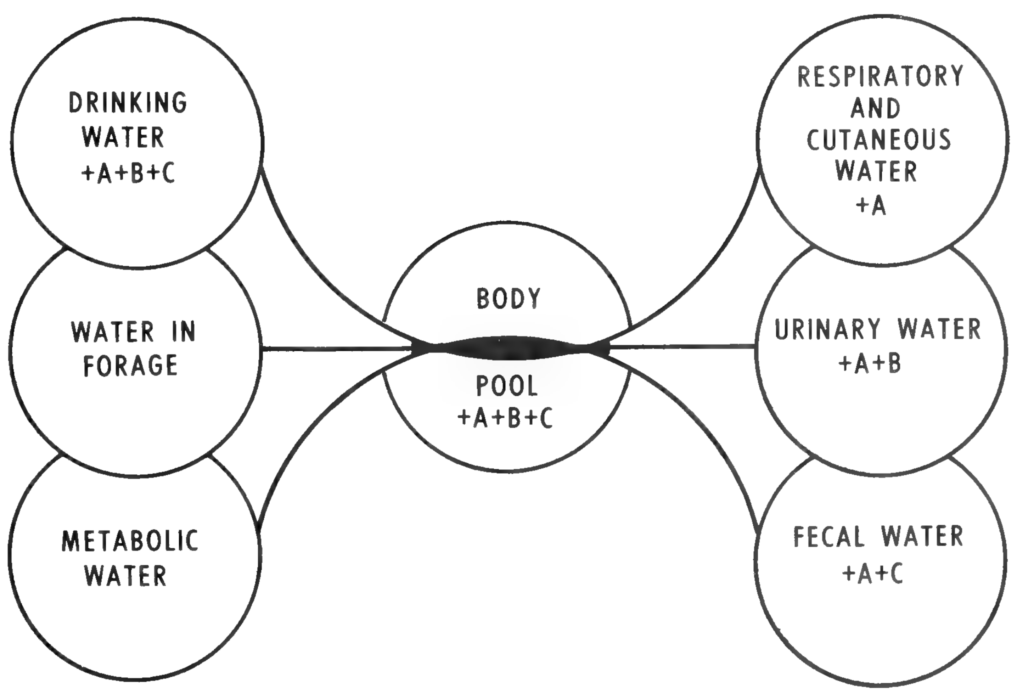

Figure 1.

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Stomach Content Analyses: A Comparison of the Rumen vs. Esophageal Techniques[1]

RICHARD W. RICE[2]

Grazing animals have the opportunity to determine their dietary intake through selective grazing. Where a choice exists, they may prefer certain species of plants. They are also capable of selecting more palatable portions of plants. The capability of animals to eat selectively has been emphasized by Bredon and Marshall (1962), who found that cattle consumed a nutritionally superior hay than that offered. Animals have much greater opportunity for selection while grazing mixed vegetation. Therefore, it has been difficult to define the botanical and chemical composition of diets of grazing animals.

The diets of grazing animals have been studied by visual observation of the plants grazed (Halls 1954; Smith et al. 1959; Reppert 1960), stomach content analyses (Martin and Korschgen 1963), analyses of fecal material for fragments of plants eaten (Croker 1959; Stewart 1967), simulation of diet by hand plucking (Edlefsen et al. 1960; Cook 1964), and clipping and analyzing pastures before and after grazing (Peterson et al. 1956; Carter et al. 1960).

These methods have not been entirely satisfactory for determining the exact chemical and botanical composition of the grazing animals' diet. Ruminant animals are particularly difficult to work with, since the mixing, rechewing, and selective passage of dietary materials through the digestive tract may confuse or bias analyses of stomach contents or of fecal material. The rumen contents of grazing animals contain the residues of certain forages eaten as much as 10 days before sampling, whereas certain other components of the diet may remain in the rumen for only short periods. Thus, stomach and fecal analyses may be seriously biased toward more fibrous or less digestible materials in the diet. Norris (1943) found large variability between the botanical analysis of the forage fed and the botanical analysis of the rumen ingesta of sheep.

The success of the quantitative determination of animal food habits depends on an exact knowledge of the botanical and chemical content of the diet. Fistulation techniques seem to be the methods chosen. The purpose of this article is to discuss ruminal-and esophageal-fistulae techniques for obtaining samples of a grazing animal's diet.

DEVELOPMENT AND USE OF ESOPHAGEAL FISTULAE

The technique of esophageal fistulation is not new. It was reported in 1855 by Claude Bernard; Pavlov conducted studies with dogs in 1889 (cited by Van Dyne and Torell 1964). The use of this technique has been hindered by difficulties associated with esophageal anatomy (McManus 1961). The esophagus does not have an enclosing serosa; it has a poor blood supply; the fistulation restricts the necessary movement of the esophagus; and scar tissue that further restricts the function of the musculature often forms. Food blockage often occurs, and animals will die if it is not removed. In some cases the muscular tone and action of the esophagus is impaired, and the animals cannot swallow ingested food. The cannula may be expelled; extensive salivary loss and serious dehydration may occur within a few hours.

Various surgical techniques have been described;[3] the procedures used at the Wyoming Station were similar to those of Van Dyne and Torell (1964).

Closures for the fistula have generally been of two types, a permanent cannula (Cook et al. 1958; Rusoff and Foote 1961) or a removable plug (Van Dyne and Torell 1964; McManus 1962). The removable plug has been used at the Wyoming Station, since a larger opening is maintained and a more complete collection of ingested food is possible. The size of a fistula is important. Blackstone et al. (1965) obtained a more complete collection of ingesta from sheep with a larger opening.

In early developmental stages of esophageal surgery, animal losses were great. For instance, McManus (1962) established fistulae in 35 sheep and found that only 5 were suitable for field studies, and Torell (1954) had success with only 1 of 4 sheep. Cook et al. (1958) were able to use three of four sheep; however, they lost all of a second group of four fistulated sheep for various reasons. Cook et al. (1961, 1962) have used fistulated sheep successfully under range conditions. Lesperance et al. (1960) were unsuccessful with 4 esophageal-

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[3] Torell 1954; Cook et al. 1958; Hamiliton et al. 1960; McManus 1962; Chapman and Hamilton 1962; Cook et al. 1963; Van Dyne and Torell 1964.

fistulated steers. Van Dyne (1962) has reported good success with steers and sheep. Other workers also have used the esophageal fistula in cattle and sheep for diet sampling.[4] The Wyoming Station has used the esophageal fistulae in sheep (Blackstone et al. 1965; Strasia 1968) and cattle (Jefferies 1968) with good success. In one study (Strasia 1968) esophageal-fistulated sheep were used to study diet habits on alpine range. They were left unattended for up to 1 month without supervision. No losses occurred due to fistulation.

The esophageal technique has not been used appreciably with wild ruminants because the collection of ingested forage samples requires that the animals can be caught easily and that their normal grazing habits be disturbed as little as possible. A deer has been fistulated at the Engeling Wildlife Management Area at Tennessee Colony, Tex.,[5] but the animal has so far not been used for diet collections.

DEVELOPMENT AND USE OF RUMEN FISTULAE

The rumen fistula is a permanent opening into the ruminal-reticular area of the animal. It is usually placed in the paralumbar fossa on the left side of the animal where the rumen lies very close to the outer wall. This type of fistula is easy to establish and to maintain. It apparently has little if any effect on the normal functioning and activities of the animal (Drori and Loosli 1959).

The use of the rumen-fistulated animal for the collection of diet samples has been described.[6] The procedure involves the complete emptying of the rumen of the collector animal. After the animal has grazed for a period of time, the rumen is again evacuated. The collected material then undergoes botanical and chemical analyses.

The rumen fistula technique has limitations. It is restricted to cattle or to other large ruminants; it involves time and effort for the operator to remove 20-50 gallons of rumen ingesta before sampling. The physiologic effect of an empty rumen must be considered. The removal of the rumen contents must stimulate an immediate influx of fluids from other body spaces and may initiate a strong stimulus for food intake. With the urge to fill the empty rumen, the animal probably grazes in an abnormal pattern, and may be much less selective than normal. Emptying the rumen as seldom as three times weekly had a depressing effect on the digestibility of forage in rumen-fistulated animals (Lesperance and Bohman 1963).

Taylor and Deriaz (1963) circumvented some of the problems of esophageal rumen evacuation by obtaining ingested boli of food at the esophageal orifice. An attendant caught ingested boli by walking alongside a rumen-fistulated animal while it was grazing. This system limits the distance traveled by the animal and the number of animals which can be handled conveniently.

Except for the research by Lesperance et al. (1960), the rumen evacuation technique has not been compared with esophageal fistulation for sampling the diet of grazing animals. The esophageal and ruminal fistula samples were similar in chemical composition, however, the esophageal samples contained more nitrogen-free extract.

BOTANICAL ANALYSES OF FISTULA SAMPLES

There are many methods of estimating the botanical composition of the grazing animal's diet (Ward conference paper). The samples collected by either the rumen or esophageal fistula method should be comparable. These are usually collected in bolus form, saturated with saliva, and partially chewed. There may be large particles of feed mixed with small fragments. Care should be taken so that these samples are not contaminated with regurgitated feed. Cook et al. (1958) found that browse plants could be identified in fistula samples, whereas grass species were too finely masticated for visual appraisal.

Heady and Torell (1959), using a microscopic-point technique, found that trained personnel could make identifications with a minimum of error. Malechek (1966) depended upon a microscopic technique for identifying finely ground fragments from rumen-fistulated steers.

Van Dyne and Heady (1965) reported that the grazing habits of cattle and sheep were different. Sheep selected a higher quality diet containing more forbs and grass leaves than did cattle. Where quantitative botanical analysis of the diet was desired, large numbers of animals were required because of variability among animals in diet selection. However, for a reasonable number of animals, the diet could be accurately sampled.

In a Wyoming study (Strasia 1968), sheep selected a diet which contained a greater proportion of forbs than grass early in the grazing season: 73 percent in July, 52 percent in August, and 40 percent in September. The nitrogen content of the diet declined as the forb content decreased; however, the fiber, lignin,

[4] Torell 1954; Bath et al. 1956; Weir and Torell 1959; Edlefsen et al. 1960; Chapman and Hamilton 1962; Arnold et al. 1964; Hoehne et al. 1967.

[5] Personal correspondence with G. H. Veteto and R. M. Robinson, Engeling Wildlife Management Area, Route 1, Tennessee Colony, Tex., 1968.

[6] Lesperance et al. 1960, Shumway et al. 1963, Cable and Shumway 1966, Malechek 1966.

and *in vitro* dry matter digestibility of the diet was relatively constant. Percent composition was as follows:

	July	Aug.	Sep.
Nitrogen	3.6	2.1	1.7
Fiber	43.7	41.2	45.4
Lignin	9.9	10.1	8.3
In vitro dry matter digested	42.4	42.8	43.5

This tabulation indicates that the sheep grazed selectively and maintain a relatively constant quality of diet. They adjusted to differences in forage availability and quality by changing their species preferences.

When using fistula collection procedures, investigators are able to determine the preferences of grazing animals for species of plants under many conditions and types of range.

CHEMICAL ANALYSES OF FISTULA SAMPLES

Ruminal or esophageal fistulae were developed primarily to define the chemical composition of the grazing animal's diet. During collection, forage samples are thoroughly wet and mixed with saliva. Saliva is composed of water, minerals, and possibly nitrogen (McDougall 1948). Cook (1964) found that saliva increased moisture, ash, and nitrogen in the forage collected by esophageal fistulae. Lesperance and Bohman (1964) and Blackstone et al. (1965) also reported an increased nitrogen content in forages as a result of salivary contamination during esophageal collections. Several other workers,[7] however, did not report this condition.

Salivary contamination of fistula-collected forages with phosphorus has also been reported,[8] while calcium contamination has not been observed (Lesperance et al. 1960; Hoehne et al. 1967).

The composition and amount of saliva secreted by fistulated animals varies with the diet. Dry, coarse feeds stimulated a greater salivary flow than succulent feeds (Lesperance et al. 1960). Somers (1961) and Bailey and Balch (1961) found that the nitrogen content of saliva was related to the nitrogen content of the diet. In Wyoming, Blackstone et al. (1965) observed that the salivary ash content was greater when esophageal-fistulated sheep ate lush forage than when they ate dry forage. More moisture was added to a dry grass sample, while more ash was added to the fresh grass when collected through an esophageal fistula:

	Before collection	After collection	Amount added
Fresh grass:	*Percent*	*Percent*	*Percent*
Water	62.7	85.0	22.4
Ash	8.3	11.7	3.4
Nitrogen	2.8	3.0	.2
Grass hay:			
Water	9.3	82.0	72.7
Ash	4.7	7.7	3.0
Nitrogen	1.4	1.8	.4

The dry matter, ash, and nitrogen content of saliva from steers maintained on native hay or alfalfa pellets (Cundy and Rice 1968) was as follows:

	Hay fed	Pellet fed
	Gm./100 ml.	*Gm./100 ml.*
Dry matter	1.13	1.13
Nitrogen	.005	.010
Ash	1.04	1.04

Saliva from steers maintained on native hay (8 percent protein) had a slightly lower nitrogen content than saliva from steers maintained on alfalfa pellets (18 percent protein). Esophageal samples collected from the alfalfa pellet-fed steers tended to have higher nitrogen contents and lower ash and lignin contents than those collected from steers fed native hay:

	Hay fed	Pellet fed
	Percent	*Percent*
Dry matter	13.2	13.1
Ash [1]	11.4	13.1
Nitrogen [1]	2.9	2.7
Cellulose [1]	30.6	28.1
Acid detergent lignin [1]	2.0	2.7

[1] Dry matter basis

Since saliva adds considerable ash to esophageal samples, some investigators have proposed that the chemical composition of esophageal samples be reported on an ashfree basis (Cook 1964; Hoehne et al. 1967).

The method of handling esophageal samples after collection also appears to affect the chemical analyses. The fiber and lignin content of forages may be increased by drying samples at high temperatures (Van Dyne and Torell 1964; Smith et al. 1967). A combination of temperature and moisture apparently causes a nonenzymatic browning reaction that increases the apparent fibrous content of feeds (Van Soest 1962). The soluble carbohydrates in plant material are lost rapidly unless the sample is frozen soon after collection. The soluble components of the diet may also be lost if saliva is allowed to drain off samples or if saliva is squeezed or rinsed out of the samples (Langlands 1966; Arnold et al. 1964; Hoehne et al. 1967). Smith et al. (1967) compared the effect of freeze drying with drying at 60° C. on the chemical analyses of esophageal fistula samples. They found that fiber and lignin were higher in the samples dried at 60° C.

[7] Lesperance et al. 1960; McManus 1961; Lombard and Van Schalkwyk 1963; Arnold et al. 1964; Langlands 1966; Hoehne et al. 1967.

[8] Lombard and Van Schalkwyk 1963; Cook 1964; Langlands 1966; Hoehne et al. 1967.

In work in Wyoming,[9] esophageal samples of forage dried at 60° C. were significantly lower in ash than samples frozen after collection. The nitrogen, cellulose, and acid-detergent lignin contents were not significantly affected by sample preparation:

	Frozen *Percent*[1]	Dried *Percent*
Ash[2]	19.3	12.3
Nitrogen[2]	2.9	2.8
Cellulose[2]	32.2	29.9
Acid detergent lignin[2]	2.3	2.4

[1] Means with different superscripts are significantly different ($P<.01$).
[2] Dry matter basis.

Also, dry matter was significantly reduced and ash was significantly increased when samples of alfalfa were collected through esophageal fistulae in steers; acid-detergent lignin tended to be higher. Rinsing the esophageal samples with tapwater further reduced the dry matter. Rinsed samples had significantly higher cellulose, lower ash, and lower nitrogen than esophageal samples analyzed without rinsing. The rinsing of esophageal samples had a large effect on the chemical constituents of samples:

	Before collection[1] *Percent*	After collection[1] Not rinsed *Percent*	After collection[1] Rinsed *Percent*
Dry matter	52.3[a]	14.6[b]	11.4[c]
Ash[2]	8.4[a]	16.8[b]	7.8[a]
Nitrogen[2]	3.24[a]	3.0[a]	2.5[b]
Cellulose[2]	30.2[a]	28.0[a]	31.8[b]
Acid detergent lignin[2]	1.49[a]	2.2[a]	2.5[a]

[1] Means with different superscripts are significantly different ($P<.01$).
[2] Dry matter basis.

DETERMINATION OF DIET DIGESTIBILITY

Once a representative sample of the diet has been collected, the digestibility may be determined by the use of the artificial rumen (Barnes 1965; Johnson 1966; Van Dyne 1962). The *in vitro* artificial rumen techniques currently in use may be classified generally into two types: (1) microbial digestion of dry matter or cellulose and (2) a two-stage system where preliminary microbial digestion is followed by an acid-pepsin treatment to remove the effects of microbial or forage protein (Tilley and Terry 1963). The *in vitro* or artificial rumen is very useful for predicting the *in vivo* digestibility of forages and complements the collection of diet samples by fistulated animals. The rate of fermentation *in vitro* is apparently related to the voluntary intake of forages (Donefer et al. 1960). Digestibility data coupled with estimates of fecal excretion can give reliable estimates of intake of forages. If the botanical composition of the diet is known, the intake of individual species of forage may be estimated. Similarly, when the chemical composition of the diet is known, nutrient balances may be determined.

[9] Cundy, D. R., and Rice, R. W. 1968. Salivary contamination by esophageal collection with steers. (Unpublished data). Univ. Wyo., Laramie, Wyo.

SUMMARY

The diet of grazing ruminants can be sampled by using fistulated animals. In this way the animal itself expresses its preference for plant species or portions of plants. The use of esophageal fistulas is preferable to the use of rumen fistulas because rumen evacuation (1) subjects the experimental animals to unphysiologic conditions, (2) is limited to large animals, and (3) is more laborious. Although complete botanical identification of fistula samples is possible, the variation within animals in their selection of plant species limits the accurate estimation of the contribution of plants making up a minor portion of the diet. The botanical analysis of fistula samples will yield quantitative information about animal preferences for the major species of the diet.

Chemical analyses of fistula samples are complicated by salivary additions during collection. Saliva adds moisture and minerals, and may or may not add nitrogen to the collected sample. The composition and amount of saliva added to fistula samples varies with the nature of the diet. Collected samples must be handled carefully because rinsing, drying, drainage of excess saliva, and other procedures preparatory to analysis will affect chemical constituents. The fibrous analysis appears to be affected least, whereas the effects of collection and handling on nitrogen, phosphorus, and soluble carbohydrate analyses may be considerable.

Fistula collection is the best method now available for obtaining quantitative information about the botanical and chemical nature of the diet of grazing animals.

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Stomach Content Analyses: Collections from Wild Herbivores and Birds

DEAN E. MEDIN[1]

Estimating dietary consumption of wild herbivores and birds by examining material found in their digestive tracts has been a technique applied by professionals for more than a century. In 1858, Jenks analyzed the contents of robin stomachs in Massachusetts, and he has been considered the American pioneer in the method. Beal, Cottam, Forbes, McAtee, Judd, Barrows, Lantz, Kalmbach, Wetmore, Gabrielson, Merriam, and Sperry in the United States and Prevost, Schleh, Rorig, Herman, Gilmour, and Collinge in Europe were prominent early workers (Kalmbach 1934; Martin et al. 1951).

During the pioneering period, interest lay primarily in determining the economic status of bird species and in giving popular recognition, understanding, and protection to birds. These objectives were apparently well attained (Davison and Hamor 1960). Leopold (1933), Kalmbach (1934), and Errington (1935a) expressed the need for further and expanded observation and experimentation, not only with birds, but with other animal groups, particularly with those animals involved in the rapidly developing field of wildlife management.

McLean (1928), Dixon (1928 and 1934), Forbes and Bechdel (1931), and Hosley and Ziebarth (1935) undertook early studies of dietary consumption in deer. Dixon's work in California remains a classic study in the use of observational methods to estimate animal diets. Forbes and Bechdel may have been first in publishing results of stomach examinations in wild ruminants. Errington (1932) and Dalke (1935) reported new techniques of studying raptor and upland game bird food habits. Foods eaten by predaceous mammals began to receive attention about the same time (Errington 1935b; Murie 1935).

From these beginnings have come greatly expanded and more refined approximations of animal diet. Analysis of stomach contents, or contents of other divisions of the digestive tract, has continued to be a useful technique for these approximations.

SOME USEFUL REFERENCES

Errington (1932 and 1935a), Cowan (1945), Kalmbach (1954), Julander (1958), Talbot (1962), and Gullion (1966) are a few who have pointed out the significance, application, and continuing need for dietary research.

Recent studies applying digestive tract analysis methods include those of Dirschl (1963), Boag (1963), Talbot and Talbot (1963), Ward (1964), Bishop and Hungerford (1965), Anderson et al. (1965), Pulliainen (1965), Rogers and Korschgen (1966), Kolev (1966), Bear and Hansen (1966), Irving et al. (1967), Scotter (1967), and Bradley (1968).

Specialized study objectives, anatomical and trophic differences between animal groups, various limitations not subject to investigator control, and the constant search for new and improved methods have stimulated application of techniques other than analyses of digestive tract contents. Some have been used independently; others have been used as supplemental or correlative approaches.

Adams (1957), Hungerford (1957), Hercus (1960), Hegg (1961), Storr (1961), Adams et al. (1962), Lay (1965), Korschgen (1966), Kiley (1966), and Stewart (1967) examined fecal material.

Observation of browsing or utilization has been carried out in various forms (Julander 1937 and 1958, Deen 1938, DeNio 1938, Dasmann 1949, Smith 1952, Smith and Julander 1953, Smith 1954, Webb 1959, Crouch 1966, and Severson and May 1967).

McLean (1928), Dixon (1934), Hahn (1945), Buechner (1950), Saunders (1955), Cole (1956), Harry (1957), Wilkins (1957), Lovaas (1958), Knowlton (1960), White (1961), Harper (1962), Lamprey (1963), Davison and Sullivan (1963), Ahlen (1965), Dzieciolowski (1967a), and Harper et al. (1967) observed free-ranging wild animals or examined feeding sites following feeding activity. Free-ranging tame or semitame animals were observed at close range by Buechner (1950), Wallmo (1951), Dunkeson (1955), Brown (1961), McMahan (1964), and Dzieciolowski (1967b).

Confined animals have been used in estimating food requirements and forage preferences. Forbes and Bechdel (1931), Maynard et al. (1935), Davenport (1937), Nichol (1938), Smith (1950), Smith and Hubbard (1954), Dahlberg and Guettinger (1956), Alkon (1961), Brown (1961), and Duvendeck (1962) have successfully used confinements to obtain such estimates for deer. Useful data from captive animals have been obtained by Nestler et al. (1945), Jensen and Korschgen (1947), Arnold (1942), and Currie and Goodwin (1966) with jackrabbits, Michael and Beckwith (1955) with bobwhite quail, McFarland and

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George (1966) with geese, Carleton (1966) with sciurids, and Tietjen et al. (1967) with pocket gophers.

Techniques using enclosures (Crouch 1966), exclosures (Webb 1959), and photography (Greenwalt and Jones 1955) have also been of value in appraising diets. Den (Errington 1937) and roost or nest debris (Errington 1932), rodent feeding sites (Takos 1947), and cheek pouches of some rodents (Johnson 1961; Bradley 1968) have been used as additional sources of food habits data.

METHODS OF HANDLING MATERIAL

Methodology in the study of animal diets has been treated in some detail by McAtee (1912), Cottam (1936), Glading et al. (1943), Hartley (1948), Martin (1949), Martin and Korschgen (1963), and Dzieciolowski (1966).

Collection

Observation of the contents of stomachs, intestines, crops, gizzards, gullets, and proventriculi have all provided dietary information. Frequently several of these contents are observed to improve estimates. Sometimes the entire digestive tract of small mammals and many birds is collected and preserved. Crops of gallinaceous birds and doves are preferable to gizzards because such contents will not have been exposed to the more destructive digestive processes. In many studies, both crops and gizzards have been analyzed. Gullets of waterfowl sometimes contain food particles in suitable condition for appraisal.

It is often impractical to save the entire stomach contents of larger herbivorous animals, and a sample, commonly about a quart, is removed. Among ruminants, samples are generally taken from the rumen or rumen-reticulum. Contents are either mixed prior to sampling or samplings are taken from several parts of the food mass.

Dietary composition in domestic livestock has been appraised by use of fistulated animals (Heady and Torell 1959; Van Dyne and Heady 1965; Cook et al. 1967; and others). A similar approach in ruminant game animals, although admittedly much more difficult, may offer compensating rewards. The difficulties inherent in fistulating and maintaining an animal with physiological and psychological characteristics far different from those of more docile domestic animals can be appreciated. Successful rumen fistulation has been reported for deer by Short (1962) and Dziuk et al. (1963). Both rumen and esophageal fistulation techniques are currently being investigated for use on tamed or penned animals.[2]

[2] Personal correspondence with A. Lorin Ward, Apr. 30, 1968.

Flushing tubes (Vogtman 1945; MacGregor 1958) induced regurgitation (Errington 1932), and stomach pumps [2] are also used to obtain food materials for analysis.

Establishment of Sampling Limits

The number of samples gathered for analysis should be a major consideration in animal food studies if diets are to be reliably estimated. When sample sizes are too limited, results may be of questionable validity. When data are summarized by season or other units of time, sampling adequacy is further lessened. The contents of a single stomach or crop may appreciably distort findings. How sampling limited in time can alter conclusions was clearly demonstrated by Korschgen (1958), who found widely divergent food habits in mourning doves for a given month in different years.

Because knowledge of dietary habits of some of the less abundant animal species is lacking, and because sample material for analysis is difficult to acquire, results based on only a few specimens have been reported. Errington (1932) did not regard stomach analyses as providing the best quantitative estimate of raptor food habits, at least partly because the number of stomachs examined that were representative of a given set of conditions was often too small to have much mathematical significance. The limitations of small samples should be recognized and interpreted accordingly.

Apparently, only a few workers have been much concerned about the number of samples required for reliable estimates. Davison (1940) compared results obtained from examination of 4, 9, 18, 95, and 471 bobwhite crops. Data obtained from 95 crops were essentially the same as those from 471 crops. Korschgen (1948) reported similar results and concluded that a minimum of 100 bobwhite crops should be obtained from a large area of similar plant growth to provide a representative sample. Anderson et al. (1965) used statistical methods recommended by Hanson and Graybill (1956) to estimate sampling adequacy in mule deer stomach content analyses. A sample size of 93 provided an adequate estimate of major food items within 15 percent of the true mean at the 95 percent confidence level. Van Dyne and Heady (1965) calculated the number of fistulated sheep and cattle required to sample dietary constituents within a desired level of precision by the procedure of Stein (1945). The number of animals required to estimate dietary composition within 10 percent of the mean with 90-percent confidence was variable, depending on animal class, grazing period, and dietary component. Generally, many animals

were required for sampling the diet for most botanical constituents.

Samples must often be acquired from animals dying of causes unrelated to the collection of data. It is questionable whether such samples provide a reasonably unbiased estimate of diet. Few data are available on this point; however, Leach (1956) reported little difference in percentage composition of rumen samples taken from winter-killed deer and samples collected by shooting.

Animals vary in the diet they select from one location to another, from one season to another, and even from one year to another (Korschgen 1958; Boag 1963). The diet chosen may also vary over a period of a few days (Nichol 1938) and within the same day (Van Dyne and Heady 1965). Perhaps less apparent, diets may vary among individuals. Individual animal selectivity has been demonstrated for deer (Duvendeck 1962), mourning doves (Davison and Sullivan 1963), sheep (Heady and Torell 1959), and cattle (Van Dyne and Heady 1965). Hancock (1950) found certain sets of monozygotic twins more discriminating in dietary selection than others, whereas both members of a given set of twins showed about the same degree of selectivity. Nichol (1938) recognized individual preferences among deer, but noted that over a long period individual selection tended to follow group patterns.

Differences in diet related to sex (Dalke 1938; Loveless 1959) and age (Boag 1963; Harper et al. 1967) have also been reported.

Individual variation in food selection could have a significant influence on the results of studies using limited numbers of experimental animals. Feeding trials conducted without adequate numbers of test animals would appear particularly susceptible to bias.

Preservation

Sample material is preserved by drying, refrigeration, or immersion in chemical preservatives. Refrigeration can preserve both the color and texture of stored materials. Formalin, generally a 4- to 8-percent solution, is the most reliable and economical chemical preservative for stomach, intestine, and crop materials. A 70-percent alcohol solution has been used for gizzards of small passerine birds.

Segregation

Partial segregation of materials recovered from digestive tracts is frequently accomplished by rinsing the sample through sieves of various mesh sizes, or, if minute particles are important, through fine mesh bolting cloth. Some have achieved segregation by floating or decanting items of different size or specific gravity. Arata (1959) used a technique based on differential sedimentation of food particles of varying sizes and weights. Occasionally, sample materials can be better examined without washing or sieving, for example, contents of bird crops or small mammal cheek pouches.

Final segregation is most often done by meticulous sorting and separation, using forceps. Separation may be accomplished with either wet or dry material, depending on the nature of the sample, the method of storage, and the investigator's preference.

The limits to which final segregation is carried are not well defined, but these are probably determined by the composition of the sample material, the judgment of the investigator, and practicalities of time and economics. The volume or weight of unseparated residue may be measured, and proportions of constituent items may be visually estimated; the residue may be proportioned on the basis of identified materials, or it may be discarded as unidentifiable. Often only the larger fragments, which constitute a small fraction of the original sample material, are segregated and eventually identified.

Courtright (1959) criticized estimation of ruminant food habits on the basis of only the larger and grossly identifiable fragments. He found that proportional composition of caribou rumen materials caught on 11 different sieve sizes (4 to 200 meshes per inch) varied appreciably in relation to different plant groups. Composition of large "identifiable" plant material was not comparable with that of smaller particles. Confirming evidence with caribou was provided by Bergerud and Russell (1964) and Scotter (1966). Dirschl (1962), however, presented contrasting results with antelope rumen material, finding very little difference in the composition of items remaining on three mesh sizes (3.5 to 7 meshes per inch).

Identification

Accurate identification of ingested food items is a difficult yet critically important stage in a dietary analysis. Procedures and methods used in the identification process are discussed in detail elsewhere in these Proceedings.

ASSESSMENT AND PRESENTATION OF RESULTS

Various quantitative expressions have been used to appraise and describe dietary consumption. Tabulation of the numbers of each food item found, statements of the frequency with which each type of food was found to occur, and estimates of food mass by weight or volume measurement are most commonly used.

Several forms of point analysis have been used to provide estimates of volume, weight, and composition of food samples.

The most appropriate method of assessment and presentation of data has been one of the controversial issues in the study of animal foods (Hartley 1948). Diversity of opinion began early (Beal 1897; McAtee 1912) and, to a lesser extent, continues (Jensen and Korschgen 1947; Brown 1961; Dirschl 1962; Scotter 1966). Various methods have been rejected because these imperfectly depict food consumption by means of a single quantitative expression.

Number Tabulation

Tabulation of numbers of food items alone has been criticized as not being a sufficiently comprehensive indication of diet (McAtee 1912). Certain foods, such as carrion, fruit pulp, sap, and fragmented vegetable material, cannot be assessed numerically, nor can allowance be made for different sizes of food items. A record of food items taken, however, remains an appropriate and acceptable method of appraisal for some purposes. Numbers of prey taken are often emphasized in studies of predaceous species (cf. Gross 1944).

Occurrence Tabulation

A statement of the frequency of occurrence of food items has been used by many investigators and is considered an important interpretive index. In some studies it has been used exclusively (cf. Johnson 1961), but it is more often associated with other descriptive expressions. Gilfillan and Bezdek (1944) believed that a record of food-item occurrences provided a more accurate picture of ruffed grouse food preferences than did volumetric data.

Volume Measurement

Volumetric methods of appraisal were employed early in the development of food-habits research (McAtee 1912), and volume continues to be perhaps the most consistently applied descriptive statistic. Volumes may be estimated visually by assigning relative percentage proportions to sample materials or may be measured directly by water displacement in various sizes or modifications of graduate cylinders (Martin 1949). The method employed depends on the nature of the sample material. Volume of discrete and readily segregated items may be measured by water displacement. Percentage calculations based on visual estimates are made when food items are so small, mixed, and fragmented as to make segregation impractical, or are too large or irregular to fit into glass graduates.

Martin et al. (1946) compared the "aggregate percentage" and "aggregate volume" methods of summarizing data. Aggregate percentage methods are used when volumes are estimated and percentages are the only figures available. Aggregate volume summaries can be used when volumes are actually measured and expressed in cubic centimeters. Most investigators have used one of these two methods, and some (cf. Ward 1964) have used both.

Hartley (1948) and Beck (1952) discussed some of the shortcomings of volumetric analyses and, along with others (McAtee 1912, Swanson 1940, Martin 1949, Brown 1961, Talbot and Talbot 1963, Martin and Korschgen 1963), pointed out the limitations of any single quantitative description and the desirability of using two or more complementary expressions.

Weight Measurement

Assessment by weight has been considered the more laborious and more refined method of presenting food-habits data. Apparently until comparatively recently, only Rorig (1903) had expressed results by weight. Recent literature indicates more interest in using weight appraisals (Norris 1943; Jensen and Korschgen 1947; Saunders 1955; Dirschl 1962 and 1963; Scotter 1966 and 1967). Objections to gravimetric methods have been summarized by Hartley (1948) and Beck (1952). Martin and Korschgen (1963, p. 327) point out that weighing segregated materials after drying under conditions of controlled temperature and humidity "cannot eliminate all sources of error and has the handicap of requiring additional time and expense," as compared to less refined methods of appraisal.

Norris (1943, p. 246), however, used weight as "a more logical measure than volume in addition to eliminating error in estimating volume percentage." Scotter (1966) concluded that gravimetric methods offered several advantages over volumetric analyses in a caribou food habits study. In addition to being more rapidly determinable, weight values could be more easily related to forage yield and utilization studies and to nutritive content values obtained by chemical analysis of forage, since these values are usually expressed in terms of air-dry weights.

Point Analysis

Chamrad and Box (1964) describe an adaptation of the point quadrat, often used in sampling vegetation, to estimate volumetric composition of rumen contents. Comparisons with known volumes were within acceptable limits of error provided sample material was adequately mixed and there were no large items with unusual surface texture in the mixture.

Volume percentages were estimated directly from point contacts.

Heady and Torell (1949), Lesperance et al. (1960), Lusk et al. (1961), Van Dyne and Heady (1965), and Galt et al. (1966) used "microscopic point" or "laboratory point" methods to estimate botanical composition of ingesta retrieved from fistulated cattle and sheep. Collected material is systematically passed under a binocular microscope equipped with a cross-hair. Species and plant parts under the cross-hair are identified and recorded as a hit. Percentage-point data may be converted to weight by regression.

DESCRIPTIVE INDEXES

In the search for better ways of presenting and interpreting results of wildlife food studies, various descriptive indexes have been devised. Some that have received particular attention equate food availability with consumption or combine single estimators of diet so as to better describe the relative importance of food items.

Glading et al. (1940) were perhaps the first to examine food availability-consumption relationships. During a period when the diet of the California quail consisted almost entirely of leaf material, a "desirability coefficient" was developed based on the percentage volume in the total diet, the percentage occurrence in quail stomachs, and the percentage of the species in the plant population:

$$\text{Desirability coefficient of a food item} = \frac{\begin{array}{c}\text{Percentage volume}\\ \text{of this food in}\\ \text{the total diet}\end{array} \times \begin{array}{c}\text{Percentage of stomachs}\\ \text{in which this}\\ \text{food occurred}\end{array}}{\begin{array}{c}\text{Percentage of this species}\\ \text{in total plant population}\end{array}}$$

The coefficient was relative and only indicated the choice between species available at the time.

Bellrose and Anderson (1943) obtained a numerical rating of certain waterfowl food plants by dividing the percentage plant use by the percentage of plant abundance. An index rating of 1.0 for a food plant indicated utilization approximately in proportion to its abundance; a larger figure indicated a greater food plant value; and a smaller figure indicated a lesser value. Similar consumption-abundance ratios have been used in studies of deer (Hill 1946; Chamrad and Box 1968), elk (Harper 1962), pocket gophers (Ward and Keith 1962), and sheep and cattle (Van Dyne and Heady 1965).

Hungerford (1957) combined a measure of food availability with food utilized in a "food index":

$$\text{Food index} = \frac{\text{Percentage utilization} \times (100 - \text{percentage availability})}{100}$$

where percentage utilization equals percentage occurrence of various food items in grouse droppings and percentage availability equals percentage occurrence of food items in plot studies on the same brood range. The index is based on the assumption that a food item eagerly sought by grouse but limited in abundance has a higher relative value than a food item commonly available and used with equal frequency. Availability is expressed in opposition to utilization in order to properly weight the index.

To express numerically the relative importance of plants eaten by black-tailed deer, Cowan (1945) derived a "consumption index" —the mean percentage volume of a plant species in the stomach contents during a seasonal period multiplied by the number of months represented and totaled over the four seasons. The resulting approximate figure was an index of the relative bulk contribution of individual forage species to annual forage consumption.

Beck (1952) introduced a "food-rank index" that combined percentage, volume, relative weight, and percentage occurrence of food items found in turkey crops:

Index number = Volume of the food item in percent × Frequency of the food item in percent × Specific gravity of the food.

Later (Beck and Beck 1955) a nutritional value was added to the basis formula.

Baumgartner et al. (1952) developed a "volume-frequency index" wherein the positioning or rank of a food item as indicated by the volume index and the rank expressed by the frequency index were combined as a simple average:

$$\text{Volume-frequency index} = \frac{\text{Volume rank} + \text{Frequency rank}}{2}$$

Both volume and frequency data are equally weighted in deriving the index.

Major mule deer food items were graphically summarized by Anderson et al. (1965) as an "adjusted ratio." The mean percent volume and frequency index of food items were equated as a product of the two expressions. Volume and frequency estimates were accorded equal weights in the ratio product.

SOME LIMITATIONS OF THE METHOD

Examination of digestive-tract contents provides estimates of the kinds of food taken

by animals and may indicate the relative proportions in which food items are consumed. However, the method is not without its limitations.

The fact that certain foods are digested more quickly and more thoroughly than others creates problems in evaluation. Although this difficulty was recognized by early food-habits workers (cf. McAtee 1912), it remained largely unassessed. Davison (1940) compared food items found in the crops and gizzards of bobwhite quail and concluded that the crop was the only part of the alimentary canal in which food items remained in the same proportion as in the food eaten. Jensen and Korschgen (1947), however, found that even in crops, proportions of foods differed appreciably from those fed.

A controlled-feeding study with sheep by Norris (1943) has been frequently cited to indicate limitations of stomach content analyses as a quantitative estimate of forages consumed. Differential digestion was apparent, and percentages of food items found in the stomach were poor estimates of items consumed. Only the larger, readily identifiable plant fragments were segregated and used, however; this procedure has more recently been criticized by Courtright (1959), Bergerud and Russell (1964), and Scotter (1966).

Bergerud and Russell (1964) compared rumen contents of four sacrificed caribou fed known rations from 30 minutes to 72 hours before death. Their findings revealed that identifiable fragments of some food items disappeared quickly from the rumen, and digestion rates varied between plant groups and to some extent between species within groups. Plant fragments retained by sieves with a 0.078-inch mesh size were separated and used in calculating digestion ratios.

Limitations imposed by differential digestibility, although not directly investigated, have been recognized by other workers (Errington 1932; Hartley 1948; Smith 1952; Cole 1956; Jensen 1958; Davison and Hamor 1960; Edwards and Ritcey 1960; Brown 1961; Martin and Korschgen 1963; Anderson et al. 1965; and Scotter 1967).

Most investigators have accepted digestive-tract analysis methods as providing a reasonable estimate of at least the kinds of food consumed. The validity of even qualitative results has not been accepted without question. Rumen content analysis of caribou (Murie 1933) and mule deer (Anderson et al. 1965) did not reveal food items known to have been taken.

Partially digested foods are not only likely to have undergone substantial alteration of their original proportions, but they are also more difficult to identify. Hill (1946), Martin (1949), Brown (1961), and Anderson et al. (1965) have mentioned limitations of identification. Dietary analyses are tedious and require patience and considerable study. The quality and accuracy of results depend on the person(s) making the examination. Investigator error in food-habits studies is apparently largely unassessed.

Recognition of limitations imposed by digestive-tract analyses has promoted use of correlative methods. Dixon (1934), Deen (1938), DeNio (1938), Hahn (1945), Buechner (1950), Smith (1954), Wilkins (1957), Lovaas (1958), Brown (1961), Bishop and Hungerford (1965), and Chamrad and Box (1968), are but a few who have used field methods to complement laboratory analyses or, conversely, used digestive-tract material to supplement field observations.

Utility

Imperfections of method and lack of precision in results have not prevented digestive-tract examination from being a useful and widely applied means of investigation. Kalmbach (1954, p. 276) maintained that "Whenever we are seeking the identity of food items . . . or whenever we aim to determine merely the presence or absence of particular items of diet, analysis of stomach contents is the only direct and reliable method of approach." Recognition that findings are only approximations (Martin 1949) does not nullify the value of the method. Under some conditions (Talbot 1962; Dirschl 1963), stomach analysis is the only method feasible.

The method has been found applicable in several related, yet distinct kinds of studies. Evaluation or appraisal of the "economic" status of animals (McAtee 1933; Gross 1944; Lumsden and Haddow 1946), environmental damage (Cole 1956; Cole and Wilkins 1958; Ward and Keith 1962; Browning and Lauppe 1964), predator-prey relationships (Errington 1932; Murie 1935; Robinette et al. 1959), animal competition (Halloran and Kennedy 1949; Davis 1952; Morris and Schwartz 1957; Julander 1958; Sparks 1968), life histories (Dixon 1934; Buechner 1950; Murie 1951; Loveless 1959), ecological relationships (Rasmussen 1941), environmental manipulation (Martin and Uhler 1939; Hungerford 1957; Biswell 1961), food palatability (Bellrose and Anderson 1943; Cowan 1945; Hill 1946), animal preference (Deen 1938; Hill and Harris 1943; Talbot 1962; Chamrad and Box 1968), poisonous foods (Forbes and Bechdel 1931; Buechner 1950; Bak and Lewandowski 1959), animal condition (Harris 1945; Anderson et al. 1965), food quality (Lehmann 1953; Bissell 1959; Klein 1962), dependence on supplemen-

tal feeds (Doman and Rasmussen 1944), and differential range use (White 1960) are perhaps but a few of the applications.

RECOMMENDATIONS

Considerable knowledge about animal diets has been accumulated. However, the need for greater refinement, intensification, and diversification is apparent. Better techniques are needed to provide unbiased estimates of *what* an animal has eaten. Beyond this, we need to know more about what foods are available to subject animals and *where* and under what conditions various food items are consumed. We need to know more about *when* certain foods are taken, particularly in relation to periods of animal stress and varying physiological demands, and about *why* some foods are preferred over others. We need to know much more about how dietary findings *relate* to both the environment and the animal.

What is Consumed?

A list of the foods consumed by an animal is incomplete as a contribution to our knowledge of animal diet. Information relating consumption to the foods available for consumption is a much more valuable contribution. Many early studies were deficient in this regard. More recent investigators have attempted to correct this deficiency and to relate relative consumption to relative availability (cf. Morris and Schwartz 1957; Loveless 1959; Ward and Keith 1962; McMahan 1964; Harper et al. 1967; and Chamrad and Box 1968). Estimates of food availability, however, have generally been limited in scope and intensity. Current investigators of animal diets should attempt to obtain more precise estimates of availability, based on adequate samples, and use an estimator comparable to that used for consumption.

Microscopic identification of digestive-tract material appears to be a more refined and perhaps a less biased approach to estimating dietary consumption for some animals. Procedures employed by Malechek (1966), Sparks (1968), and Sparks and Malechek (1968) seem particularly promising: small subsamples of rumen material were first ground and then mounted on slides, and the components were identified by comparing reference slides of diagnostic epidermal tissues under a compound microscope.

Particular parts of food items consumed have not received much emphasis in many studies. Others (cf. Dixon 1934; Hill 1946; Van Dyne and Heady 1965) have presented rather detailed lists of plant parts consumed as well as plant species and plant groups. The part of the plant selected could be of more significance than the species eaten.

Poisoning among wild animals may be more of a problem than is realized. Case and Murphy (1962) concluded that research on poisoning is comparatively recent and offers many opportunities for valuable work.

Statements of probability, tests of comparative data, and statistical descriptions of variability are rarely reported in food-habits literature. Variability estimates may be useful in evaluating results and as an aid in determining sample sizes in future work. As an objective, presentation of at least minimal descriptive statistics and probability estimates would not appear to require excessive labor.

Where is it Consumed?

Smith (1952), Hosley (1956), Boag (1963), and others have indicated that dietary findings generally have local application. Cowan (1945) pointed out that palatability ratings are applicable only under the precise conditions existing when they were calculated and that their transfer by inference to other areas where different conditions prevail can lead to erroneous conclusions. Errington (1932, p. 76) suggested that digestive-tract examinations "at best show only what individual animals in a given locality have eaten at a given time. At worst they show only part of what individual animals have eaten some place, some time . . ." and that "local application . . . is one of the primary aims of food habits research." Difficulties of extrapolation may require investigations within specific localities, sites, or ecologic communities if reliable and applicable data are to be obtained. . . . Also, careful, complete descriptions of prevailing environmental conditions should be an important segment of any food-habits investigation.

When is it Consumed?

Studies of animal diets have frequently been limited in conception and in time. For example, samples obtained during a single season from hunter-killed animals only provide a fragmentary picture of diet. It should be recognized, however, that some studies, by design, have concentrated on only a single seasonal period of specific interest and have resulted in valuable contributions. Nevertheless, more studies crossing the entire seasonal spectrum are needed. Insight gained from knowledge of yearlong diet adds depth and may serve to define problems previously unrealized.

It is uncommon to find food studies representing more than 1 or 2 years of research. Gullion (1966) criticized short-term studies as providing an insufficient understanding of food requirements under different and changing conditions. Korschgen (1958) pointed out

the ease with which misleading conclusions may be drawn from samples limited to a single season or year. If differences over time are to be evaluated and understood, sampling must continue for reasonably long periods.

Seasonal diets are usually reported according to some arbitrary division of the calendar. Winter (January-March), spring (April-June), summer (July-September), and autumn (October-December), or similar compartmental arrangements are often used. Some refinement in definition of diet periods to orient them more closely with seasonal changes in both the foods and their consumers would be profitable. It is important to know the developmental stage of a food item at the time of consumption. Also, the physiological state of animals undergoes periodic changes during an annual period. These periodic changes could influence dietary selection.

During certain times of the year, or in some years compared to others, animals may undergo periods of stress. Diets may be modified during these critical periods. Access to foods may be difficult or may change with changing environmental conditions. Periods of drought (Errington 1937; Korschgen 1958), flood (Loveless 1959), deep snow and low temperatures (DeNio 1938; Harris 1945; Hill 1946; Leach 1956; Morris and Schwartz 1957), high population pressure (Scheffer 1951; Hosley 1956; Jensen 1958); food failure (Goodrum and Reid 1962), and fluctuating rainfall (Baumgartner et al. 1952; Napier 1963; Anderson et al. 1965) modify the kinds and amounts of food available to the consuming animal. Additional and expanded studies are needed to sample animal diets during critical periods.

Why is it Consumed?

Animals select from available foods. Some foods are more palatable and are preferred over others that may be available in equal quantity. Answering the *why* of food consumption is much more difficult and complex than answering the *what, where,* and *when*. The subject has an extensive literature and has been reviewed by Heady (1964). He listed five factors influencing relative food preference: (1) Palatability, (2) associated species, (3) climate, soil, topography, (4) kind of animal, and (5) animal physiology. Heady's statement summarizing Cowlinshaw and Alder (1960) appears particularly applicable.

> "The act of selecting food is undoubtedly influenced by all four [groups of factors] and can only be finally understood in terms of interactions among them. Unfortunately, most studies to date have concentrated on single factors, or even more simply, just recording the magnitude of preference."

Why certain foods are more palatable than others is also poorly understood. Studies oriented toward explaining variability in food palatability and in animal preference offer many research opportunities.[3]

What are the Relationships?

The influences on animal diet are apparently many, complex, and interrelated. Emphasis must be placed on ecological relationships if dietary data are to have the most meaning. Evaluation of the effects of variable and changing environmental conditions is essential. The influence of climate and weather, fluctuating food availability, seasonal and annual changes, animal competition, population pressures, environmental manipulation, and factors influencing choice or selection among food items by animals of different sex, age, and condition must be recognized and interpreted. The associations between dietary consumption, food quality, and animal physiology have only begun to be understood. Greater depth of interpretation and a more critical examination of relationships can improve the value of a technique that has had both historic and current application.

[3] Longhurst, W. M., Oh, H. K., Jones, M. B., and Kepner, R. E. A basis for the palatability of deer forage plants, Thirty-third N. Amer. Wildlife and Natu. Res. Conf. Trans. 1968. (in press).

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Stomach Content and Fecal Analysis: Methods of Forage Identification [1]

A. LORIN WARD [2]

INTRODUCTION

The food habits of wildlife in the United States have been studied by examining digestive tract material for more than a century. The primary interest of the pioneering studies was to determine the economic status of bird species. Results of these first studies prompted investigation of other wildlife. Inauguration of Federal Wildlife Food-Habits Research in 1885 started an organized laboratory approach to the field. Names associated with the early work were Barrows, Beal, Cottam, Forbes, Gabrielson, Judd, Kalmback, Lantz, Martin, Merriam, Sperry, and Wetmore. The early work is summarized in "American Wildlife and Plants" (Martin et al. 1951).

The scientific study of food habits is essential to an intelligent understanding of our wildlife and domestic animals. Knowledge of the foods used by specific animals is basic to the management of their population and environment. This paper reviews and evaluates methods and techniques of identification and measurement of plant materials found in the digestive tract and fecal samples of herbivorous animals.

GENERAL REVIEW OF LITERATURE

Many workers have examined stomach contents to determine foods eaten by foraging animals. Three good references on food-habits methods and techniques are Martin et al. (1951, Martin and Korchgen (1963), and Dzieciolowski (1966a). Work with rodents has been done by Baumgartner and Martin (1939), Keith et al. 1959), Kelso (1934), Myers and Vaughan (1965), Tevix (1953), Ward (1960), Ward and Keith (1962), Williams (1962), and Williams and Finney (1964). Rabbits have been investigated by Dusi (1949), Bear and Hansen (1966), Hayden (1966), and Sparks (1967). Animals in the Cervidae family have been studied by many people. Stevens (1966), Murie (1951), and DeNio (1938) reported work on elk. Chamrad and Box (1968), Dzieciolowski (1966b), Korschgen (1962), and Leach and Hiehle (1957), to mention a few, worked with deer. Bergerud and Russell (1964) worked with Newfoundland caribou. Dirschl (1962) and Cole and Wilkins (1958) studied the food habits of antelope. Talbot and Talbot (1962) reported work on African ungulates. Stomach contents, collected by killing domestic sheep, were reported by Norris (1943). Heady and Torell (1959) and Van Dyne and Heady (1965) analyzed materials collected from esophageal fistulas. Food habits of cattle, by examination of samples from either esophageal fistulas or ruminal fistulas, have been reported by Galt et al. (1966), Harker et al. (1964), Heady and Van Dyne (1965), Malechek (1966), Shumway et al. (1963), Torell (1956), and Van Dyne and Heady (1965).

Dusi (1949) first studied food habits of herbivorous animals by histological analysis of feces. He developed procedures which were better adapted to herbivores than earlier methods used by Baumgartner and Martin (1939) to analyze squirrel stomach contents. Martin (1955) used the features of leaf cuticle in feces to assess the botanical composition of the diet of sheep grazing on heather in Scotland. Croker (1959) tested the value of Martin's (1955) method for sheep on two types of tussock grassland in New Zealand. Hercus (1960) reported on further work in New Zealand. Storr (1961) used microscopic analysis on feces of quokkas (*Setonix brachyrus*) in Australia to determine their diet. Adams (1957) and Adams et al. (1962) proposed a method of estimating the diet of snowshoe hares (*Lepus american bairdii*) by using recognition items found in the feces. Hegg (1961) examined fecal speciments from red deer (*Cervus elaphus*), chamois (*Rupicapra rupicapra*), and roe deer (*Capreolus capreolus*) from the Swiss National Park. Kiley (1966) used the microtechnique of fecal analysis to invesigate the feeding habits of waterbuck (*Kobus defassa* Ruppell and *K. ellipsiprymnus* Ogilby) in the National Parks of Uganda and Kenya. Stewart (1967) examined the qualitative potential of the technique of identifying fragments of grass leaf epidermis in feces. Eight species of palatable grasses with clearly separable characteristics were used so that misidentifications could not affect the results. The seven species of semitame animals were: Wildebeest (*Cannochaetes taurinus*), Coke's hartebeest (*Alcelaphus buselaphus cokei*), Grant's and Thomson's gazelles (*Gazella grantii* and *G. thomsonii*), buffalo

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(*Syncerus caffer*), steinbuck (*Raphicerus campestris*), and common zebra (*Equus burchellii*).

In more recent studies, there is a general trend to gather more detailed information about food supplies and feeding activities of the animal. Good examples of studies on foraging animals to illustrate this point include the work on pocket gophers by Ward and Keith (1962), on deer by Korschgen (1962) and Chamrad and Box (1968), on sheep by Heady and Torell (1959), on steers by Galt et al. (1966), and on sheep and cattle by Van Dyne and Heady (1965). It is difficult to judge the real significance of diet composition without detailed information on availability and related factors. When more detailed information is gathered on what foods are available in the areas used, it is much easier to identify food particles and to interpret results.

COLLECTING AND PRESERVING THE SAMPLE

Records of Sample

For any study of food habits it is desirable to have a record card printed for convenience in tabulating data. The author has found the 5- by 8-inch manila card with double holes punched around the periphery to be satisfactory. In some cases, the use of overlay templates with standard forms and optical mark page readers as described by Loveless (1966) could be used.

Care of Sample

Collection and storage of samples can play an important part in the success of a study. Complete records of collection data are usually kept with the sample by the use of vulcanized-fiber-paper labels or tags. Plastic bags of good strong quality make ideal containers for all types and sizes of stomach contents and feces. Materials that can be examined within 24 hours generally need no preservation. If contents can be washed and dried, they can be stored for long periods. Preservation of food materials by refrigeration is recommended. Portable ice chests and styrofoam boxes can be used in the field, and food freezers can be used in the laboratory. Freezing has the special advantage of preserving both color and texture.

Formalin is the most reliable and economical chemical preservative. Small-to-medium-sized stomachs should be preserved with a 4 percent solution of formalin (commercial formalin diluted with 25 parts of water). A stronger preservative, such as 8 percent formalin, is needed for larger specimens. Care should be used in handling formalin so that it does not contact the skin or eyes. Specimens preserved in formalin can be handled safely after placing them for 3–5 minutes in a deformalizing solution prepared from 1 gallon of tap water, 252 grams of sodium bisulfite ($NaHSO_3$), and 168 grams of sodium sulfite (Na_2SO_3).

The importance of methods and timing of stomach content collections from herbivores and birds will be covered by Medin (1968) in this conference.

For fecal analysis, collection must be restricted to fresh fecal materials. Studies have shown that it takes from a few hours to 10 days for food to pass through herbivores. Due to weathering of fecal materials in the field, it is desirable to collect fecal samples from observed animals. This will eliminate mistakes in aging, and destruction of plant parts by insects, bacteria, and fungi. It will also permit collection from individual animals. The fecal material should be stored in plastic bags to prevent drying. Refrigeration is an ideal way to store samples. It keeps the material fresh and avoids hardening and molding.

Since there is usually a large supply of each sample available, only a subsample is collected. Analytical procedures prohibit examination of all materials, and storage becomes a problem if large samples are collected. For practical reasons, sample data collected from many different fecal groups are more valuable than detailed examination of all material in one dropping. By mixing the fecal material and picking random subsamples, a representative sample can be obtained in the field. Further subsampling and mixing is done in the laboratory.

IDENTIFYING PLANT PARTICLES

Equipment

Good microscopes are essential for food-habits analyses. The widefield, par-focal dissecting binocular scope with both the fixed stand and the horizontal, swing arm mounted on a heavy base is recommended. A compound microscope will be necessary for conducting studies where plant microtechniques and histology are required.

When purchasing microscopes, include the camera accessories so that photomicrographs can be taken. Polaroid cameras work very well for developing a reference collection of photomicrographs. The 35-mm. cameras, with a fine-grain film, are good for making photomicrographs where several prints of the same photo are desirable. The new single-lens cameras with built-in light meter are ideal for this kind of work. All the major microscope companies have the necessary accessories to adapt the ordinary 35-mm. field camera to their microscopes.

Other useful items include forceps, scalpels, sieves, petri dishes, measuring graduates, metal scoops or funnels, and shallow enamel pans. Funnels covered with bolting cloth are used to strain fine materials. An oven is helpful for drying materials.

The work is time consuming and tiresome, so good equipment, situated in comfortable surroundings, is important for obtaining good results.

Reference Materials

There is no substitute for a good reference collection. Its size should depend on the scope of the study. Preliminary observations and familiarization with the animal and its feeding behavior are also necessary. A reference collection may be made while collecting feeding behavior and food-availability data. All materials in a reference collection, regardless of size, should bear authentic identification.

Reference collections for forage identification studies should include not only herbarium specimens of plants, but also collections of seeds, buds, and underground parts such as bulbs and tubers. For most studies conducted over several months' time, it will be necessary to collect plants in various stages of development. Collections at different times during the year are also necessary to be sure early- and late-maturing species are included.

Preparation of Reference Materials and Unknowns

Many animals grind their food into very small fragments. Reference material must be prepared so it illustrates microscopic characteristics. Baumgartner and Martin (1939) published a paper on the use of plant histology as an aid in squirrel food habits studies. Kelso (1934) also used this method in studying pocket gopher stomach contents. Dusi (1949) discussed methods for the determination of food habits by plant microtechnique histology and their application to food habits of cottontail rabbit. Others who have used this microscopic technique include Keith, Hansen, and Ward (1959), Ward (1960), Ward and Keith (1962), and Myers and Vaughan (1965) on pocket gophers; Davies (1959) on identification of grasses in leafy stage; Mulkern and Anderson (1959) and Brusven and Mulkern (1960) on grasshoppers; Williams (1962) on microtine mammals; Heady and Torell (1959) and Martin (1955) on sheep; Lesperance et al. (1960), Ridley et al. (1963) on steers and heifers; and Van Dyne and Heady (1965) on cattle and sheep.

Techniques for preparation of reference materials for feces examinations are usually the same as those used to identify stomach contents. Hercus (1960), Storr (1961), Stewart (1965), and Stewart (1967) present descriptions of procedures they used. In some cases, reference materials were prepared from plants after they had passed through the animal.

Various methods have been used to make microscopic slides of reference materials. Dusi (1949) described in detail methods for mounting plant epidermis that could and could not be removed by mechanical means. He used rinses of Formalin-Aceto-Alcohol and stained the tissue in Mayer's Haemalum, which was described by Johansen (1940). His slides were mounted in Apathy's gum syrup as described in Richards (1943).

Maceration slide mounts were made from plants whose epidermis could not be mechanically stripped off. Plant tissue was placed in a vial with equal parts of 10 percent nitric acid and 10 percent chromic acid, freshly mixed, heated at 40° C. for 6 to 24 hours (depending on the plant), rinsed in water, stained with Mayer's Haemalum, and then mounted in Apathy's gum syrup on glass slides. Baumgartner and Martin (1939) used Hertwig's solution, a combination of clearing and mounting fluid. It can be prepared by using the following formula:

19 cc. HC1 added to 150 cc. water
60 cc. glycerine
270 g. chloral hydrate crystals

Croker (1959) macerated the leaves in 50 percent nitric acid over a water bath, and the tissues were then washed in water to remove the acid. The cuticle was gently separated from the rest of the leaf with mounted needles and a camel-hair brush. It was then floated onto a slide with a fine jet of water and a brush. The slides were taken through the alcohol series from 15 to 95 percent, stained with 1 percent acid fuchsin, and permanently mounted in Euparal.

A simpler method has been used by the author to prepare reference slides. Leaf, stem, and root materials, from either fresh plants or herbarium mounts, were soaked in water until soft. A small segment of plant tissue was held on a glass slide and scraped on both sides with a sharp scalpel. A few drops of Hoyer's solution were applied, and the fine plant fragments were separated with a needle.

Hoyer's solution can be made by the following formula:

20 percent gum arabic
35 percent distilled water
12 percent glycerin
30 percent chloral hydride
3 percent glucose

For permanent mounts, these slides were heated in an oven at 40° C. for 48 hours.

Williams (1962) stained materials with 1

percent hematoxylin solution to help bring out the identification features of plant fragments in microtine stomach contents.

Reference photomicrographs of plant tissues will help greatly in the identifications. Black and white photomicrographs are used, mainly because of cost and use in publications. Color transparencies are good for teaching aids and for illustrating work in slide talks.

Stomach contents or fecal materials can be examined dry or wet. The method used depends on the way the material has been stored and on individual preference. I prefer them fresh and wet. If the contents are fresh or have been frozen, they are first washed in water to rinse off digestive juices. If formalin has been used, the contents should be rinsed in running water. Fresh materials do not break into small fragments as they often do when dried.

Identification

Identification of food items is difficult and critically important. Experience and judgment are significant assets in identification. Many times, especially with large animals, a good sample of leaves, twigs, stems, or seeds can be selected; the sample should be easily identified and should help in the identification of the smaller fragments. The classifications should be as specific as possible. However, broad classifications are important. In many studies, the material listed as unknown could at least be classified as plant, animal, or soil. When working with herbivores, for example, classification into broad groups, such as grasses, forbs, or shrubs, is often possible, and such information is important.

In food-habits studies of grasshoppers, rodents, rabbits, sheep and cattle, the microtechnique and histology methods have been used. These methods have been particularly useful when working with small animals and ruminents that grind their food into small fragments. The first step is to study reference material to become familiar with known plant histology. Time thus spent will not be wasted. A key based on distinctive differences in stomata, hairs, cell configuration, size, and other morphological characteristics can be made to help in identification.

A procedure of analysis cannot be standardized for all species of herbivores. These species are many sizes and eat and chew their food in many ways. For elephants, the food material may be separated with a fork; for seed-eating birds, the seeds can be separated by screens or by hand picking; for small mice, separation of plant fragments may not be practical. To satisfy all conditions, the procedures have to be modified and restricted.

The amount of time required to train an individual to do examinations depends on the methods being used, the animal being studied, and the experience and interest of the person. Material collected from the fistula of a cow is much easier to work with and identify than plant fragments from a pocket gopher stomach.

Galt et al. (1966) reported that it took 24 hours to take 1,600 points and 6 hours to take 400 points by the microscopic-point method described by Heady and Torell (1959). These identifications undoubtedly were made by an experienced worker. Students examining pocket gopher stomachs and Wiley-milled material from rabbit stomachs and cattle fistula have commented that it takes about 2 months of intensive study of reference material before moderate progress is made in identifying plant fragments. The speed and efficiency improve with experience. It is advantageous for the person doing the examinations to participate in the collections.

The reference collection should be consulted frequently. There are no good illustrated reference publications for plant fragments. Herbarium specimens collected from study areas are the most useful and provide more accurate identification. An important aid in the identification of seeds is the Seed Identification Manual (Martin and Barkley 1961). A collection of known seeds is better.

The first few stomach contents in any study will be the most difficult to identify. Do not spend a lot of time trying to identify puzzling fragments. Often, after the larger or more characteristic items are identified, close examination shows that the finely divided materials are parts of the larger, already identified food items.

The extent of segregation of food items varies with the investigator, objectives, and the method of analysis being used. For purposes of this discussion, the methods will be considered on the basis of the magnification used to identify food materials.

No Magnification or Very Low Power

Naturally, this method has limitations. For example, small rodents that grind their food into very fine fragments cannot be studied by this method. Food habits of large herbivores and birds are very often examined without the aid of high magnification.

Various methods have been used to segregate materials from large herbivore stomachs. It has always been questionable what should be done with the unidentified mass of finer items. Some workers separate the coarse items by use of one-eighth inch mesh sieves, and do not use the fine materials in their analysis (Dirschl 1963; Cole 1956; and Cole and Wilkins 1958).

Others measure the mass of finer items and relate the proportions of coarse identified material to this quantity, assuming that the fine material is made of the larger items in the same relative amounts (Norris 1943; Saunders 1955). Usually the volume or weight of this unsegregated fine material is measured, and the proportions of its constituent items are estimated visually (Korschgen 1962). To help in this estimate, it is often advisable to separate small samples into small individual piles of known materials.

Dirschl (1962) tested the results of screening antelope rumen contents through 5.66, 4.00, and 2.83-mm. sieves, separating the materials on each screen into species, and then weighing them and determining percent composition. He found very little difference in the mean composition between these three mesh sizes. The use of the 5.66-mesh size saved considerable time. Sieve mesh sizes of 0.078, 0.0328, and 0.0164 inch were evaluated in the analysis of Newfoundland caribou rumen foods (Bergerud and Russell 1964). They concluded that the larger plant fragments were not representative of the entire rumen contents because of differential digestion between plant groups. Scotter (1967) tried to determine which of three sieve-mesh sizes could best be used to determine composition of forage samples from 20 barren ground caribou rumen. He found that data obtained from any one mesh size could be inaccurate and misleading. The proportion of lichens generally increased as the mesh size decreased, and grasses increased as the mesh size increased. He combined data from three screens for each sample.

Norris (1943) analyzed stomach contents of sheep fed controlled diets. There were some serious variations in his results, and these are often cited. There were also weak points in his method that should be pointed out. No finely comminuted particles which passed through a window screen were identified or separated, and only the particles that were readily identifiable on the screen were used in the analysis. A representative sample of 2 percent of the total on the screen was taken, and all the readily identifiable particles were picked out with forceps. As a result, over half of the stomach contents consisted of material too fragmentary for separation or identification, and these were not used in the analysis except that it was considered to have the same composition as the larger, recognized and weighed material. This large amount of unidentified material could have accounted for the wide variability in the results.

Another point that should be considered is the difficulty and added work of basing all analysis on a weight basis. Digestion starts as soon as the plant is eaten. The readily digested materials are immediately dissolved. They are usually in the form of liquids or fast-dissolving substances that do not account for a large volume, but are heavy. They would not introduce a great amount of error, but should be considered in trying to justify the added work of drying materials for a weight measurement.

Analyses using very little magnification have been used by many biologists. All of the early workers in the Fish and Wildlife Service, U.S. Department of the Interior, recognized the limitations imposed by this method, and they promoted the use of field methods to supplement the results of laboratory examinations. The usual procedure is to save the fine particles and to attempt to identify and segregate a small subsample to at least classify the material into the broad groups such as grass, forbs, or browse. Some workers examined this fine material under higher magnification to determine if they were missing any important food items that were going through the screens. Although the method has limitations and the results are approximate, the technique is still widely used and provides useful information.

There is not much in fecal material that can be recognized without the use of magnification. For predators and reptors, many food items can be recognized from tooth or bone fragments. Herbivore feces are too fine for identification unless the food material is something like whole grains whose hull comes through the animal in large pieces.

Identification Under Low-Power Magnification

Low-power magnification is also used in the screening methods of segregation. Magnification was increased in an attempt to identify and separate the fine materials. As better equipment became available, the investigator classified more of the finer materials. This not only eliminated a lot of error in the study of larger herbivores, but it permitted us to begin work on the smaller animals.

Heady and Torell (1959) introduced the terms "laboratory point" or "microscopic point" in their method of determining botanical composition on clipped plots and fistula contents of sheep from the annual type range on the Hopland Field Station in Mendocino County, Calif. They did not state what magnification they used, but in a report of similar work done later by Van Dyne and Heady (1965), it was stated than an 18-power binocular microscope was used. The microscope method was developed so that the green material from clipped plots and fistulas could be sampled by the same procedure. Eight subsamples were taken from each fistula sample. Each

subsample was spread evenly in a tray approximately 5 by 30 inches. The tray had a series of 25 notches on each side that served as stops when the tray was passed under a binocular microscope. One eyepiece of the scope had a crosshair. When the tray and material was passed under the scope, the species nearest the crosshair was considered a hit. Fifty hits were recorded from each subsample. Preliminary samples of known composition indicated that a total sample of 400 hits was necessary to obtain sample means for the major species within 10 percent of the population mean 95 percent of the time.

Other work with the microscope point technique for analysis of esophageal and ruminal fistula samples from cattle and sheep has been reviewed by Van Dyne and Torell (1964). Percentage point data for species and species groups were converted to percentage weight by use of equations developed by Heady and Van Dyne (1964). Regressions based on a similar procedure were used by Galt et al. (1966).

The adaptation of the point-analysis method to several combinations of artificially constructed populations of plant fragments and on actual rumen contents of white-tailed deer *(Odocoileus virginianus)* was reported by Chamrad and Box (1964). Their sample device consisted of a frame containing five hatpins placed at a 45-degree angle through a wooden bar. The 45-degree angle of the pins facilitated microscopic observation of pin hits. Each pin was dropped into the artificial population or rumen material spread evenly over the bottom of an enameled lab tray, and the first hit of each pin on a plant fragment was recorded. One hundred pin drops per sample were used. There were no significant differences between the abilities of two investigators to estimate the volumetric composition of the samples, nor was there a difference in the ability of the individual investigator to repeat his estimates. The point analyzer gave reliable results if (1) the rumen sample was adequately mixed and (2) there were no large items with unusual surface texture in the mixture.

Harker et al. (1964) evaluated the microscopic point method. Samples of *Brachiaria decumbens* (a coarse perennial common in East Africa) and sweet potato vice (*Ipomoea batatas*) were obtained from six esophageal-fistulated Zebu cattle. The forage was rinsed with 2 percent acetic acid to remove saliva, and then mixed by wet weight into desired portions. The method gave a satisfactory estimate of species composition on a percent dry-weight basis. Four hundred points estimated percent dry matter at the 90-percent confidence limit to within 20 percent of the mean if the weight is 16 to 30 percent, to within 10 percent of the mean if the weight is between 30 and 50 percent and to within 5 percent of the mean if the weight is 50 to 95 percent.

Van Dyne and Heady (1965) found variability among individual animals in the composition of diet. From their results based on the microscopic point technique, they calculated sample size required to estimate dietary composition within 10 percent of the mean with 90 percent confidence. In general, many animals would be required to sample the diet for most botanical constituents. More sheep than cattle usually would be required for a given constituent, and more animals of either class generally would be required in early summer, when there is a high availability of herbage, than in middle or late summer, when less herbage is available. Fewer animals are needed with more inclusive plant groups. Even for such broad plant categories as grasses, forbs, and shrubs, at least 10 animals would be required for either cattle or sheep in early summer.

Adams (1957) and Adams et al. (1962) proposed a method of estimating the weight of food eaten by snowshoe hares; using this method, the number of recognition items in the feces on an area is estimated. This number is then converted to weight eaten by calibration obtained by feeding penned hares known weights of foods and then counting the recognition items. The fecal pellets were teased apart in water and detergent, suspended in water over a grid, and scanned under a dissecting microscope at 7X magnification.

Low-power magnification has also been used in fecal examination to determine the presence of tracers for food items. Grain and fresh vegetable baits have been coated with aluminum tracer and placed in the field. Fecal pellets have been examined for the nondigestible aluminum flake to determine the distance traveled from bait sites, and the percent of the rodent population using bait.

Identification Under High-Power Magnification

Stomach analysis of small rodents that grind their food into very fine particles made it mandatory for microtechniques and histology methods to be used. These same techniques, with some modifications, have been used in food-habits studies of big game and domestic livestock. With big game animals, rumen contents are usually taken from dead animals. Samples from domestic livestock have been collected from either esophageal- (Torell 1954) or rumen-fistulated (Shumway et al. 1963; Malechek 1966) animals.

Botanical composition of stomach contents of pocket gophers was determined by washing stomach contents in cold water, screening on

silk bolting cloth, and mounting small samples on microscopic slides. Ten random spots on each slide were studied at 100X magnification, and the percentage volume of each plant was estimated (Keith et al. 1959; Meyers and Vaughan, 1965; Ward and Keith 1962). This method was also described by Williams (1962) for use in studying microtine food habits.

Hayden (1966) used a similar technique to examine black-tailed jackrabbit (*Lepus californicus*) stomach contents. He estimated percentages of each plant material on 80 fields of vision at 100X on five slides containing one-third cc. contents. Values for three slides were averaged for each animal, and individuals were averaged to make a composite monthly sample. Bear and Hansen (1966) used a similar technique in their food habits study of white-tailed jackrabbit (*Lepus townsendii*).

Malechek (1966) overcame the problem of having many different sizes of food particles in steer rumen samples by first grinding oven-dried rumen samples in a Wiley mill equipped with a 1-mm. screen. He then mounted small subsamples of the finely ground material on standard microscopic slides, and analyzed them under a compound binocular microscope at 125X. The botanical composition of each sample was determined by the relative number of epidermal fragments of each species recognized in 100 microscope fields.

Sparks (1967) used the microtechnique to study the food habits of black-tailed jackrabbits in Colorado. Contents were washed and mixed in warm water, and then dried and ground in a Wiley mill over a 20-mesh screen. The material was washed again over a 200-mesh screen to insure mixing and to remove dirt and very small fragments. One slide was prepared from a sample of each stomach content. The percentage of each food item in the diet was estimated by examining 20 systematically located fields on each slide with a binocular-compound microscope at 125X magnification. Average frequency percentages were computed for all species in the composite sample of 25 jackrabbits (500 fields). The frequency percentages were then converted to density per field (Curtis and McIntosh 1950), and percent composition of each food item was calculated for the sample.

The use of microscopic slide techniques has been evaluated, but usually in connection with large-scale food habit studies. The first work with pocket gophers by the author was done very cautiously. Known plants were fed to caged gophers, and then the animal was killed and the stomach was examined to see if the plant could be identified. A few animals were fed mixed diets of known plant material, and the validity of the microscopic method was checked.

Several recent studies have confirmed the reliability of the microtechnique for determining the vegetative composition of fistula and stomach content materials. Although he was not able to obtain samples from fistulated steers, Denham (1965) compounded forage samples from six plant species to simulate fistula forage samples, and had them examined by microtechniques. Samples were prepared for analysis by first oven drying, and then by grinding through a 1-mm. mesh. A small subsample of the material was mounted on a microscope slide. The analysis involved observing and identifying material at approximately 100 locations on each of two slides. When all six species were correlated with the percentage weight of each expected in the sample, a very significant correlation of $r = 0.97$ resulted. Denham concluded that equally high degrees of accuracy should be achieved from analysis of samples collected through esophageal fistulae.

Sparks and Malechek (1968) accurately estimated percent composition by dry weight for 15 hand-compounded mixtures of plants that are found in the diets of some herbivores. The mixtures were sampled by recording the frequency of occurrence of each species in 100 microscope fields under 125X magnification, converting frequency to density, and calculating relative density as an estimate of percent composition by dry weight. Dry weight percentages could be predicted directly from relative density. The two requirements that had to be met before frequency percentage could be converted to density were (1) that the plant fragments must be distributed randomly over the slide, and (2) that the density of particles must be such that the most common species does not occur in more than 86 percent of the microscope fields. They concluded that the microscopic technique they used is an accurate means of determining the dry weight composition of stomach samples, esophageal samples, rumen samples, and clipped herbage.

Dusi (1949) found that fecal pellet material must be mounted on microscope slides for analysis. Only fresh droppings were used. In general, he found that the contents of each of the several fecal pellets of rabbits in a dropping pile were like others in the pile unless the pellets varied greatly in color, shape, and size. Further statistical testing showed that an adequate sample consisted of about one-eighth of an average size pellet broken into particles, spread evenly over a microscope slide, and covered with a three-fourths-inch-square coverslip. Each slide was examined under a compound microscope. The identified particles were recorded and treated by frequency of occurrence methods.

Stewart (1967) examined the qualitative and

quantitative potential of the technique of identifying fragments of grass leaf epidermis in feces. The study entailed feeding experiments with captive animals. Feces weighing 70 grams (fresh weight) were collected either twice or three times a day. The feces were kept in formalin acetic alcohol (85 parts 70 percent alcohol, 10 parts 40 percent formaldehyde, and 5 parts glacial acetic acid). From each 70-gram fecal collection, a 1-gram sample was placed in 4 ml. of concentrated nitric acid in a round-bottomed flask and heated for 2–3 minutes over a water bath. This treatment clears the epidermal fragments and facilitates identification. The sample was then made up to 100 ml. with water, and boiled and stirred to complete the clearing process. After removal of the supernatant fluid, the fragments were stored in a constant volume of 1 part formalin acetic alcohol and 1 part 30 percent aqueous glycerine. From each 1-gram sample, subsamples were spread out on six slides under 3.8- by 1.9-cm. coverslips with a suitable density of fragments.

Slides were analyzed both by counting fragments and by assessing their cover. Counts were made by traversing the slide systematically at 100X magnification, and counting those fragments which fell partly or entirely between parallel lines marked on the slide. Area measurements were made, with an eyepiece micrometer, along similar traverses; those fragments or parts of fragments lying between parallel lines were measured.

The results clearly invalidate the estimation of proportion of grasses ingested by counting all fragments. This invalidation occurred because some species broke into smaller fragments and the total number of fragments was thus more numerous. Analysis by measuring the area of 100 fragments in each of three fecal samples showed considerable improvement in accuracy compared with counts. The variance was high, however, and possible causes seemed to be the presence of occasional, very large fragments, or differential separation of fragments before or after these were placed on the slide. The high variance, and the length of time required to make analysis with point quadrats, mean that it would be extremely time consuming to make sufficient analysis to reduce the standard error to within 10 percent of the mean.

Since the major constituents of the diet can be identified in the feces, quantitative data on a frequency basis, indicating the relative importance of different grasses in the diet, can be obtained.

Croker (1959) collected droppings from one sheep for each sample. These samples were diluted with an equivalent volume of water and subsampled. A thin film of material was spread between two slides, and 50 identifications were made on each of four slides, for a total of 200 identifications per sample. No special treatment or staining was necessary. The objective was to determine which species were being grazed at that particular time. The results were not intended to be a quantitative estimate.

Hercus (1960) reported on further work in New Zealand. She collected unweathered feces from the field and preserved them in formalin/acetic acid/alcohol. Three-gram samples were suspended in 100 ml. of water, and 3 subsamples were withdrawn for microscopic examination. The number of fragments of each cuticle pattern was counted and identified. She found some variation in the total count per unit volume on duplicate samples, because the cuticle fragments were not of even size or shape. To allow a quantitative estimate of intake and utilization, she felt it was necessary to relate amounts of cuticle in feces to the actual amounts of each plant species eaten, either in terms of weight or number of leaves.

Storr (1961) used the microscopic analysis technique on feces of kangaroos and wallabies in Australia to determine their diet. Feces were first dried and thoroughly ground. The sample was then boiled in 10 percent nitric and chromic acid, and fitted to a reflux condenser for 1 minute. The material was washed with water and transferred to a centrifuge tube, drained, and dyed with an alcohol solution of gentian violet. The fecal residues were then washed with alcohol and centrifuged for at least 5 minutes and drained. Slides were examined under low power (45X) by systematically traversing zones 2.8 mm. wide, whose centers were 5 mm. apart. Fragments of epidermis were identified, and their area was estimated in hundredths of a square millimeter by using a graduated eyepiece. The percentage by area of each species present was then obtained for each slide. Analysis of many slides prepared from a single sample of feces was necessary when precise information was required about the diet of individual animals. More often, information is required about a population. In population studies, only one fecal pellet from each quokka was prepared, and the composition of the preparation was based on the mean of the proportions observed in two slides. Data obtained were qualitative and quantitative because (1) there is little or no digestion of epidermis that is encased in cutin, (2) the epidermis is usually identifiable to species under low-power microscopes, and (3) the relation between the surface area and dry weight of the foliage can be determined for each species.

Hegg (1961) adapted procedures of Dusi (1949). For grass examinations he softened the fecal samples in water and then washed

them through a sieve. The particles were counted in water under a binocular dissecting microscope. For examination by microscope, the droppings were soaked in water, cooked in 10 percent KOH solution in water bath for 5 minutes, shaken, drained, and stained with Sudan III (alcohol solution) for 1 hour. The material was then mounted in glycerin gelatine or glycerine with wax edging.

Kiley (1966) prepared samples by the methods described by Storr (1961). The presence or absence of the individual species' epidermis in the feces was recorded; no quantitative data were taken. One sample was taken from each of two animals in seven different localities in three National Parks. The percentages were obtained by counting the number of fragments of dicotyledonous plant cuticles and grass cuticles per low field (100X). Ten subsamples were counted from each fecal sample. He states that the limitations of this method of estimating quantitatively the amount of dicotyledons present in the feces are well known, and these figures are considered merely as a guide for further work.

EVALUATION OF FECAL ANALYSIS METHOD

The use of a fecal examination to determine plant use certainly has value. Studies to date have found only a few species of plants that lost their identity when they passed through an animal. Qualitative data on a frequency basis was possible. The possibilities of making quantitative measurements is somewhat questionable. More studies are needed to evaluate the use of fecal analysis, particularly with different animals on different ranges.

There are a few points that can be learned from the work already completed.

1. Only fresh dropping should be used to relate animal use with time and place.

2. Freezing has been found to be a good way to store fecal samples.

3. The work is time consuming and is subject to variation. Specific information within close limits of accuracy are very costly.

4. The method has more value in providing limited information where trends and relative importance of food items are important.

5. Fecal samples are plentiful and are easily obtained. They can be obtained without the difficulties connected with stomach contents.

6. Each animal species has its own factors that will influence the results. Preliminary studies to evaluate procedures are desirable.

7. Knowledge of the habits and habitat of the herbivore being studied are prerequisite to the success of a study.

A Study on Elk Fecal Material

During the summer of 1967, the author conducted a feeding trial with two penned spike bull elk to evaluate fecal analysis to determine diet. A half-acre plot in Nelson Park on the Snowy Range of southern Wyoming was mowed with a rotary power mower at 1-inch stubble height. All cut vegetation was collected in the pickup bag of the mower. Small samples were randomly plucked from each full bag and were separated in the laboratory. The main volume of vegetation was placed in burlap bags and transported to the Sybille Wildlife Research Unit of the Wyoming Game and Fish Commission and placed in their cooler until fed.

The two elk were penned together and fed the mowed vegetation exclusively for 10 days. They ate an average of 26 pounds of air dry forage each day for each of the 3 days records were kept.

Fecal pellets were collected starting on day 5 of feeding. A small sample of fecal material was extracted from the middle of each pellet with forceps. This material was pooled, stirred in water and detergent, and filtered through silk bolting cloth. It was then placed on blotting paper for drying. While still damp, small samples were placed on microscope slides and spread in Hoyer's solution before being covered with a 24- by 50-mm. coverslip.

Each slide was examined under the microscope at 100X magnification, and percentages by volume of grasses and forbs were estimated at 10 random points on each slide. The average percent for grasses and forbs was then calculated for each slide. The percentages for the 10 slides were totaled, and an average percentage for all slides was calculated. Grasses made up 94.4 and forbs 5.6 percent of the fecal material examined.

Vegetation samples collected in the field at the time of mowing were separated by hand into grasses and forbs and air dried, and the percentages by weight were calculated. Grasses made up 94.7 and forbs 5.3 percent (forbs ranged from 3.3 to 8.1 percent for 7 bags) of mowed samples by weight.

INTERPRETING RESULTS

Subsampling From the Sample

The size of food sample collected varies with the herbivore being studied. For small rodents and most birds, the entire stomach or crop is taken. For large animals, the standard practice has been to collect a quart of food material. This sample is taken from the rumen or rumen-reticulum in ruminants. For fistulated animals, sample volumes from 1 pint to 1 quart are taken from sheep and one-half to 1 gallon

are taken from cattle. The time needed for collection depends upon the species, size of the fistula, rate of grazing, and type of forage.

When materials are segregated, the whole sample is considered. For bird crops and some large animals, the various food items can be segregated and either weighed or measured by volume. With herbivores it is usually impractical to separate the whole sample due to the large number of fine particles. The subsampling that is thus required has been approached in different ways. Lesperance et al. (1960) describes taking 10 small grab samples at random from a collected sample and examining each sample. Others (Heady and Torell 1959; Van Dyne and Heady 1965) used at least half of the fistula sample, all in one 5- by 30-inch tray, to make their microscopic point analyses. The problems of subsampling are minimized by the point methods. Complete mixing of the sample before taking the subsample is the important consideration.

A subsampling procedure is also necessary when using the microtechniques for Wiley-milled samples of fistula or stomach-content material and from small rodents and rabbits. To insure thorough mixing, the food is washed and stirred before small samples are taken for mounting on microscope slides. Each slide is limited to the amount of material it can hold. The general tendency is to use too much material. The specific amount will depend on the judgment of the investigator. When the Wiley mill is used, the amount can be quite uniform since the material is ground to uniform size.

The number of microscope slides used has varied between workers. Ward (1960) and Myers and Vaughan (1965) used one slide for pocket gophers. Bear and Hansen (1966) and Sparks (1967) used one slide for jackrabbits. Malechek (1966) used two slides of steer rumen content that had been ground in a Wiley mill. Sparks and Malechek (1968) mounted subsamples on five slides in their study. The number of slides needed depends upon the variation between subsamples. If the material is mixed thoroughly, there should be no need to mount many slides. Procedures can be checked by comparing slides from one food sample.

The method of estimating percentage dry weight in diets evaluated by Sparks and Malechek (1968) recorded positive evidence for the presence of a plant species at a location on each slide. Frequency percentages (number of fields that the species occurred in of 100 locations) were tabulated for each species. The requirements of random distribution and density of particles make it necessary to adjust the amount of material on a slide. The number of slides was determined by the difficulty of obtaining 100 fields of view at 125X magnification without creating confusion.

Subsampling is just as important in fecal analysis when using the microtechnique. Various procedures have been followed, and will vary according to the animal being studied and the time of year samples are collected. Consistency and shape of droppings change with the food being eaten. Sampling will have to be adjusted to meet the requirements of obtaining a random subsample.

Assessment and Presentation

Food-habits data have been presented in many ways. The kind of data relates to the particular type of study. For foraging animals, the expressions of quantitative data are presented as occurrence, volume, and weight. Some investigators have used the gravimetric method based on weight after drying the segregated materials under conditions of controlled temperature and humidity. This method, however, cannot eliminate all sources of error, and has the handicap of requiring additional time and expense. The use of precise —and costly—methods of analysis is unwarranted if equivalent precision or accuracy is not applied to other phases such as sampling and segregation.

Volumes of discreet and readily segregated items may be measured by water displacement. Visual estimates of proportions are made the basis for percentage calculations for small, mixed, and fragmented materials. Whatever the method used, uniform procedure is important. Martin et al. (1946) compared the "aggregate percentage" and "aggregate volume" methods of summarizing data. Aggregate percentage methods are used when volumes are estimated, and percentages are the only figures available. Aggregate volume summaries can be used when volumes are actually measured.

More recent findings by the microcopic point method have been converted to weight by regression. Stark and Malechek (1968) found that the percent composition based on dry weight of mixtures they used could be predicted directly from the relative density.

A common-sense approach to the interpretation of the results of food habits studies is necessary. It often becomes impractical to satisfy the requirements of sample size to determine plant use to a precision level of 10 percent of the mean in all studies. Such things as individual animal variation, the variable nature of grazing, the complexities that determine palatability, and the number and amount of plants used all affect results. Many times data with broader limits will meet the objectives. At the same time there is danger in using a small number of critically examined samples from only a few animals from a small range area to interpret food use over a whole range. Wildlife species that have freedom to select a wide vari-

ety of areas to feed from and plants to eat present our most challenging problems.

Converting to Practical Values

Stomach and fecal examinations indicate which foods are most important in the diet, but the foods on which the animals are subsisting are not necessarily the most preferred. The important foods are palatable and nutritious to the animal and are abundant in the habitat, while the preferred foods are those that would be eaten in the greatest amount if all were equally available. Equating food availability with consumption has been presented in several ways. The most common way is the numerical rating obtained by dividing the percentage use of a plant by the percentage of abundance. An index ratio of 1.0 for a food plant indicates utilization approximately in proportion to its abundance; a larger figure indicates a greater food plant value, and a smaller figure indicates a lesser value (Ward and Keith 1962; Van Dyne and Heady 1965). With the increased amount of data on the nutritional value of plants at the time of use, there is need for an equation that will consider this factor in the evaluation.

The main consideration of any food-habits data is its practical value. Initial information on individual species was used in life history studies. Early bird work was centered around economic status. Many studies appraised animal damage and predator-prey relationships. The more recent studies are evaluating the ecological relationships and management implications. The emphasis on range management research to find the best and most practical means to manage, improve, and maintain the productivity of forest and related lands used for grazing domestic livestock and optimum populations of wildlife have increased the importance of determining food availability, nutritional value, and use.

CONCLUSIONS

The value of knowing the foods utilized by animals is becoming very important under our present policies of land management and improvement practices. To gain this knowledge, we are studying diets in relation to food availability and nutritional value.

The accuracy and value of the work depend on the judgment and training of the examiner. Proficiency is obtained by studying the foods available. Since most of the identifications are made from small parts of plants such as seeds, leaves, flowers, or very small fragments, a good reference collection of available foods is required. This will include slide mounts and photomicrographs of cells for the microtechniques. There are no published references to cover all of the material encountered. Each worker must study known reference materials and develop keys and recognition characteristics of his own. It is a good practice to have the examiner in the laboratory participate in the field collections.

The work is time consuming and challenging. Good equipment, situated in comfortable surroundings, is conducive to good laboratory results.

Fistula techniques of field collecting diet samples and subsequent refrigeration permits work with fresh materials. We are making progress in obtaining samples from wildlife species, and techniques are being tested. Use of telemetry for tracing, immobilizing agents for capture, helicopters for transportation, and stomach pumping and fistulas for collecting samples are all possible.

The recent work being reported on the evaluation and description of methods of analysis is encouraging. The point analysis method for clipped plots and fistula collections has been found accurate and practical. Microtechniques have proven accurate and useful, particularly for identification of finely chewed or ground food.

Results of fecal analysis of ruminant animals to determine food habits have not been fully evaluated. Until more evaluation studies are conducted, conclusions from fecal examinations should not be accepted without recognizing the limitations of the method. Qualitative data are quite reliable, but quantitative data are more difficult to measure and need more investigation.

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Biological Relations of Rumen Flora and Fauna

JULIUS G. NAGY [1]

INTRODUCTION

Depending on their digestive systems, we can divide higher mammals into three general groups: Monogastrics, with small cecum such as carnivores and omnivores; monogastrics, with enlarged cecum such as many herbivores (for example, horses, beavers, and rabbits); and ruminants such as elk, deer, antelope, sheep, goats, and cattle. During their evolution, all three of these groups developed a digestive system best suited for the particular diet available to them. Monogastrics with a small cecum have the simplest digestive system: it consists of one pouch, the stomach, and usually a small cecum. Their diet is the most concentrated of the three groups and is the easiest to digest. It consists of protein, sugars, starches, fat, and comparatively small amounts of fiber. At the other extreme of specialization are the ruminants; they have a complex system consisting of a rumen, reticulum, omasum, and abomasum. The abomasum is the true glandular stomach. The diet of a ruminant is bulky, high in lignin and cellulose, and usually low in easily digestible plant materials. For these reasons cattle have roughly nine times the digestive tract capacity of man on an equal weight basis. At least half of the energy supply of the ruminant, and all of the essential amino acids, is obtained from the by- and end-products of bacterial and protozoal fermentation in the rumen. Monogastrics with enlarged cecum also depend on bacterial fermentation, but not as much as ruminants. Food is digested in the glandular stomach, and then some of the digested materials will undergo microbial digestion in the cecum.

SIGNIFICANCE OF RUMEN MICRO-ORGANISMS

Although all three digestive systems use micro-organisms, in one way or another, to produce nutrients for the host, inter-dependence between host and micro-organisms has been developed to the highest degree in ruminants. No matter what kind of a digestive system an animal has, food intake is governed by one or more of the following requirements: Food must be available at the time it is needed, it must be palatable to the animal, and it must be digestible and utilizable by the animal. Ruminants, of course, have one more important requirement: food must be digestible by the rumen micro-organisms.

The importance of studying ruminant nutrition can hardly be overestimated. Domestic ruminants occupy a predominant position in modern agriculture: most of our big game species are ruminants; and, because of their close food requirements, domestic and wild ruminants often compete.

The presence of a "fermentation vat," where billions of micro-organisms compete and work with each other and with the host, offers a unique opportunity to study a microbial ecosystem, and at the same time offers challenges for an investigator. Food must be broken down in the rumen by micro-organisms in order to pass further down to the digestive tract. Most of the ingested carbohydrates will be converted to short-chain fatty acids (acetate, propionate, butyrate, iso-butyrate, valerate, and iso-valerate) and constitute the major source of energy for the ruminant (Annison and Lewis 1959). Since most of the short-chain fatty acids are absorbed through the rumen wall and enter the bloodstream, the concentration of blood sugar in an adult ruminant's blood is about half of that found in nonruminants. Blood short-chain fatty acid levels in ruminants are higher than in monogastrics.

The presence of micro-organisms in the rumen alters the amino acid requirements of the ruminant strikingly. Because micro-organisms are able to attack nitrogenous substances from protein as well as from nonprotein sources, i.e., urea, they can supply the host, regardless of the nitrogen source, with all the essential amino acids, providing other nutrients are not limiting. Thus, the host, in contrast with monogastrics, is freed from selecting foods where the essential amino acids are already present.

One of the major functions of the rumen micro-organisms is, of course, the conversion of cellulose in the diet of the host. Since mammals do not secrete cellulase in their digestive fluids, the digestion of cellulose by rumen microbial populations enables the ruminant to live on coarse, fibrous foods on which monogastrics are unable to subsist.

DEVELOPMENT OF THE RUMEN

At birth, the digestive system of the young ruminant functions the same way as that of monogastrics. There is no rumen fermentation. Milk through the esophageal groove bypasses

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the rumen and is digested in the abomasum in the same manner as in monogastrics. The young animal, however, through association with other ruminants and through the simultaneous intake of plant materials, will soon develop a functional rumen microbial population. Once microbial fermentation begins, the rumen will develop very rapidly. While at birth, the rumen comprises only about 20 percent of the total four-part stomach (rumen, reticulum, omasum, and abomasum) capacity, at about 4 months, the rumen capacity of deer is 80 percent of the total four-stomach capacity (Short 1964).

Bryant et al. (1958) found that calves brought up on commercial starter obtained the characteristic microflora of the adult bovine at 9–13 weeks of age. The data of Lengemann and Allen (1955) suggest that the usual adult proportions of the short-chain fatty acids, the principal end products of rumen microbial fermentation, are obtained only after 6 months of age. Our data (Nagy, unpublished) show that ratios of the short-chain fatty acids of antelope fawns do not differ significantly from those of adults at approximately 4 months of age.

Factors Influencing Kinds and Numbers of Rumen Micro-Organisms

One should not think, however, that the adult rumen microflora and fauna has a rather static composition. On the contrary, it will vary throughout the life of the animal. The kind of organisms present at any given time, their numbers, and their ratios to each other will depend on various factors. Some act directly on the animal and indirectly on the microbial population of the rumen, while others act directly on the rumen environment and thus on the balance of bacterial species present (Kistner 1965). One of the dominant factors acting directly on the animal is the human influence. Human influence on domestic ruminants is rather obvious; we continuously manipulate the genetic makeup of domestic ruminants and also change their ecological distribution. For wild ruminants, selective hunting undoubtedly influenced big game species of Europe, while in the United States the ecological distribution of bison, antelope, elk, and bighorn sheep was certainly influenced by the encroachment of civilization. Physiological changes due to selective breeding can possibly influence food selection, manner of food intake, capacity of the digestive tract, and ratios of certain organs, i.e., the rumen to total body weight. Changes in geographic location of the ruminant can expose the ruminant to different climatic conditions and consequently can alter the availability of principal plant species utilized as food.

The nature of diet so influenced will, in turn, largely determine certain rumen environmental conditions, such as the amounts of available nutrients for the rumen bacteria, rumen pH, and the concentration of end products in the rumen. Thus, the nature of diet coupled with the environmental conditions the particular diet produces in the rumen, and coupled with different growth rates of micro-organisms, adaptation of micro-organisms, and different rates of microbial removal from the rumen, will ultimately determine the balance of microbial species in the rumen. Diet, of course, will be determined by a variety of the factors discussed previously; these include human influence, plant species available, food selection, etc. Pearson (1965) found that the number of a ciliate protozoa (*Entodinium* spp.) in the rumen of white-tailed deer increases during rapid vegetation growth and decreases as plants dry up at the end of the growing season.

As the food enters the rumen, depending on its chemical nature, different micro-organisms will attack it, utilize it, and produce a variety of end products which, in turn, will be utilized by other organisms and/or by the host animal. It is generally agreed that among the short-chain fatty acids produced in the rumen, acetic acid will predominate under any dietary regime regardless of the species of ruminant. However, ratios of these acids will vary according to the diet. Concentrates which are high in easily digestible plant sugars and starches will produce proportionately somewhat lower acetate and higher propionate, while diets low in the above substances and high in fiber such as cellulose and lignin will produce just the opposite effect (Annison and Lewis 1959). Wild and domestic ruminants seem to exhibit very similar patterns in this respect, which suggests that diet and not necessarily the ruminant itself will mainly determine the patterns of microbial fermentation.

Dietary changes will produce changes in the environment of the rumen such as changes in pH of the ingesta and amounts and types of characteristic metabolites; therefore, these changes will influence the types and numbers of micro-organisms present. Under a high roughage dietary regime, the pH of the rumen ingesta will be nearly neutral, and the numbers of cellulolytic bacteria will be relatively high. A diet high in concentrate and low in roughage will produce lower pH; consequently, the numbers of cellulolytic micro-organisms will also be lower. A sudden change in diet from high roughage to high concentrate could cause rather drastic changes in the microbial population of the rumen. Thus, if the diet is changed suddenly from a low to a high concentrate (containing large amounts of starch and

sugars), lactose fermenting organisms will increase so rapidly that they will become dominant and upset the normal microbial balance. So much lactic acid will be produced that the pH of the rumen will drop, and the animal may die of acid indigestion. Injection of acid has been used occasionally to defaunate animals (Warner 1961), with a loss or decrease of cellulolytic bacteria as well.

The administration of antibiotics such as oxytetracycline, chlortetracycline, and penicillin into the rumen could seriously affect many bacteria (Munch-Petersen and Armstrong 1958; Bryant et al. 1961). Some species may decrease in numbers only temporarily, while others may disappear completely (Maki and Foster 1951). In ruminant nutrition, especially when dealing with wild ruminants, we will encounter not only manmade antibiotics but also a number of natural antibiotics. Most of these natural antimicrobial agents will not influence the population of the rumen under normal dietary regime. These substances might be important, however, in determining the amounts of food the animal will consume voluntarily or under starvation conditions when only the plant species containing these substances is available (Dietz et al. 1962). An example of these antimicrobial substances are the volatile oils which are present in varying amounts in a number of wildlife foods such as sagebrush, juniper, pine, etc. These volatile oils have been known to inhibit and kill a number of rumen micro-organisms (Nagy et al. 1964; Nagy and Tengerdy 1968; Oh, et al. 1967). The recent work of Longhurst and his coworkers (Longhurst et al. 1968; Oh et al. 1967; Oh et al. 1968) indicates that plant species containing substances with the most effective antibacterial action are the least palatable to deer.

Our *in vitro* experiments (Nagy and Tengerdy 1968) on the action of volatile oils of sagebrush on deer rumen bacteria suggest that deer could consume sagebrush with its volatile oils without harm if their diet also contains other substances. If only sagebrush is consumed for prolonged periods, our results indicate that the antibacterial substances in the sagebrush will interfere with proper microbial digestion and consequently with normal energy flow.

Different growth rates of micro-organisms will also influence the numbers of micro-organisms and thus the balance of bacterial species at any given time. There are no data available on the diurnal changes in the concentration of rumen micro-organisms of wild ruminants. Data gathered on domestic ruminants suggest, however, that frequency of feeding and not time of day of feeding will influence the concentration of micro-organisms in the rumen. Some phenomenal changes in the numbers of protozoa and bacteria can be observed after feeding. The holotrich protozoa, such as the dasytrichs, can show a spectacular, thirtyfold increase (equivalent to five generations) within 7 hours after feeding (Warner 1965).

Another factor influencing the environmental conditions and thus the balance of microbial species in the rumen is the different rate at which micro-organisms are removed from the rumen. Under a normal regular dietary regime, this factor will not influence the total number of microbial species in the rumen; it will only influence the numbers of organisms at any given time. Under starvation conditions, which we can encounter with domestic range animals as well as with our wild ruminants during the winter months, removal of micro-organisms from the rumen might be a very important factor to consider. Starvation, even for only 2 days, can eliminate at least temporarily some species of micro-organisms from the rumen, resulting in lower digestion rates of sugars and cellulose. In some cases, 3 to 4 days of starvation can cause complete loss of an organism from the rumen, and a new source of infection is needed to reestablish the species (Meiske et al. 1958). Rumen protozoa, probably because of their slow rate of reproduction, are more susceptible to decrease in numbers than bacteria. Loss of certain micro-organisms can occur even under prolonged undernutrition. Which organisms will disappear will probably depend on available nutrients in the rumen, rate of reproduction of the organism, and the rate of removal of the organism from the rumen.

The importance of loss of functional rumen micro-organisms is often overlooked. We monogastrics can eat even after prolonged starvation. Our digestive juices will be present 1 day or 1 week after the digestion of the last food. The ruminant has to depend, as a first step in digesting food, on a functional microbial population in the rumen. If this functional microbial population is lost for some reason such as starvation, acid indigestion, or excessive intake of antimicrobial substances, ruminants often stop taking in food. If food is taken, no regular digestion can occur in the absence of functional rumen micro-organisms. In either case, the animal is doomed.

FOOD INTAKE AND MICRO-ORGANISMS

Another important (and, by us, neglected) difference between monogastrics and ruminants is the regulation of food intake. This also can lead to semistarvation or starvation. Regulation of food intake by monogastrics will depend mainly on the rate at which gastric juices are able to handle food constituents.

This often enables us to increase our food intake if our diet becomes less nourishing. Ruminants, on the other hand, depend on the rate at which micro-organisms can digest food constituents. Only a few hours are required to liberate sugars from the plant cells, and to attach them and convert them to useful end products for the ruminant. Cellulose and lignin, however, might stay in the rumen for a few days. As the fiber content of the diet increases, rate of digestion in the rumen, rate of passage through the digestive tract, and, consequently, food intake will decrease. Ultimately, the animal will starve or nearly starve. This condition, coupled with a gradual loss of the functional rumen microbial population, could lead to a point of no return. The animal will die even if food is offered to him.

CONCLUSIONS

In ruminant nutrition, one of the most important concepts to understand is that we are really feeding billions of micro-organisms whose digestive activities in turn provide most of the nutritional needs of the ruminant animal. Thus, our chief concern is with providing the proper foods and ruminal environment for the micro-organisms.

In the laboratory, experimental alteration of the foods and environment of the microbial populations has taught us much about the responses of the host. We have learned to apply some of these findings under feed-lot conditions to maximize the performance of the ruminant hosts (Virtanen 1966; Raleigh and Turner 1968). However, we must keep in mind that ruminants on the range are dependent upon the welfare of their rumen micro-organisms as well, and this should be considered an important part of range ecology—for domestic livestock or game animals.

Ruminant species vary in their ability to use forages with different proportions of cellulose, lignin, and other constituents, including various bacteriocidal agents. The biological relations of range vegetation and ruminant grazers are first biological relations of vegetation and rumen micro-organisms. Cattle, sheep, goats, deer, elk, antelope, and bighorns have each made specific adaptations to many kinds of vegetation. These adaptations depended upon accompanying evolutionary adaptations of the microbial populations of their rumen (Silver et al. 1959; Short et al. 1965).

Management of livestock rangelands and big-game habitat cannot proceed intelligently without an adequate understanding of the functioning of the flora and fauna of the rumen. We have only begun to acquire this understanding.

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REMOTE SENSING

Remote Sensing: Review of Principles and Research in Range and Wildlife Management

DAVID M. CARNEGGIE [1]

INTRODUCTION

Recently, much interest has been expressed in remote sensing as a tool for improving range resource inventory and analysis. In view of this increased interest, several pertinent questions have been asked: "What is remote sensing?" "Where, when, and how can remote sensing be applied?" "Can remote sensing applications provide real-time benefits in range and wildlife management and research?" This paper seeks to help answer these questions. It will first define remote sensing and then discuss basic matter-energy relationships; sensing devices; and the advantages, limitations, and applications of remote sensing. Although much has been written about remote sensing applications and basis matter-energy relationships, only a small part of the literature will be cited.

DEFINITIONS, ENERGY-MATTER RELATIONSHIPS

In its broadest context, "remote sensing" is simply gathering information about objects without coming in contact with them; for example, information-gathering by eyesight. In this context, range managers have been engaged in "remote sensing" activities for several decades: (1) Visually estimating herbage production (2) observing degree of animal use (3) making animal counts using binoculars, and (4) using high-terrain vantage points to do generalized vegetation-type mapping.

However, in this paper, the term "remote sensing" refers specifically to the recording of energy responses from objects by means of a sensing device operated at some unprescribed distance; the energy responses are recorded in a form which can be analyzed for some specific purpose. Implied in the framework of this definition is a *sensing device* (e.g., a camera), a *carrier vehicle* (e.g., an aircraft), an *energy source* (e.g., the sun), *objects* (e.g., range vegetation and soil) which interact with energy to give unique energy responses, *recording media* (e.g., light sensitive film and magnetic tapes), and remote sensing *data* (e.g., images). Also implied is the capability for extracting information (i.e., data analysis; image interpretation and measurement) from the remote sensing data.

Thus, range and wildlife managers and researchers engage in remote sensing (a) when taking ground photographs to record the visual appearance of features along a transect or in study plots and (b) when securing and using conventional black-and-white aerial photographs to make vegetation-soil maps. In either of these activities, reflected radiation (energy in the form of wavelengths of visible light) from the vegetation and soil is recorded as a photograph, and a camera is used as the sensing device.

Until a few years ago, the term "photo reconnaissance" described remote sensing activity. Then other sensing devices became available which could record reflected and emitted energy in bands other than the photographic portion of the electromagnetic spectrum. Hence, the term "remote sensing" was coined to denote all these activities.

What is Being Sensed?

Figure 1 shows a simplified representation of the *electromagnetic spectrum* composed of discrete energy units called photons. These photons are characterized as (a) moving in harmonic wave patterns, much as an ocean wave, but at the velocity of light, and (b) varying in wavelength from high-frequency, short-wave length radiation to low-frequency, long-wavelength radiation. Between these two limits, there are many spectral *bands* or regions of radiation, each encompassing a spe-

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cific range of wavelengths for which there is a sensing capability. Those broad spectral bands which are of greatest importance in remote sensing research, listed in order of increasing wavelength, are: Gamma rays, X-rays, ultraviolet, visible, near infrared, thermal infrared, microwave, and radio waves. The energy within these specific wavelength bands that is transmitted, reflected, or emitted from objects is "what is being sensed."

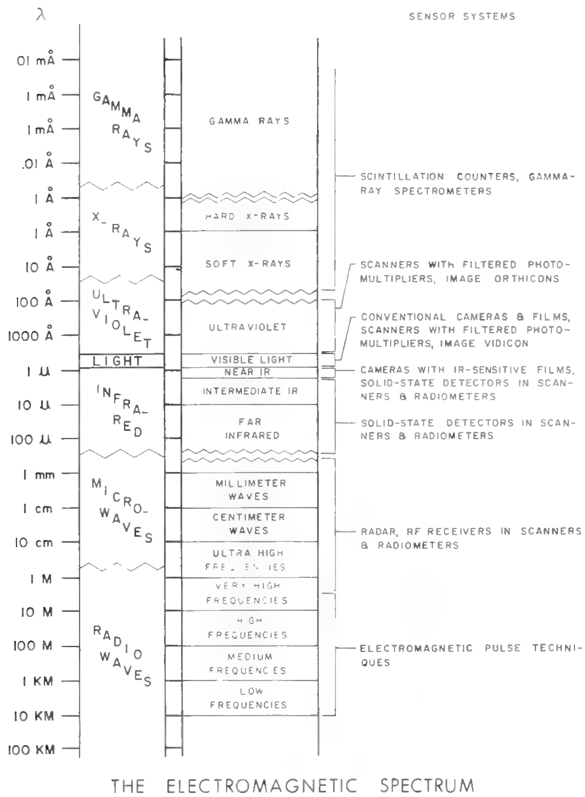


FIGURE 1. The electromagnetic spectrum with appropriate sensor systems.

What is the Source of Electromagnetic Energy?

The sun has been the main source of energy for remote sensing. In addition, all matter at temperatures above absolute zero (0° K.) radiates (emits) electromagnetic energy and hence is an energy source. Sensing devices which record reflected and emitted radiation from natural sources are called *passsive* sensing systems. Cameras and thermal infrared scanners are examples of *passive* sensing devices.

Artificial sources, such as flash bulbs and resonating tubes, also can be used as a source of energy. Devices which sense this energy are called *active* systems. Radar—which generates, transmits, and receives and records its own energy pulses—is an example of an active sensing system.

What happens to Electromagnetic Energy?

When photons of specific energy interact with matter, mass and energy are conserved in accordance with basic physical principles, and energy is either (a) *absorbed,* i.e., given up largely to heating matter; (b) *emitted* or reemitted by the matter as a function of temperature and structure (at the same or different wavelength); (c) *reflected,* i.e., returned unchanged to the medium; (d) *transmitted,* i.e., propagated through the matter or the atmosphere; or (e) *scattered,* i.e., deflected by atmospheric particles and lost ultimately to absorption or further scatter, or (f) some combination of two or more of these phenomena.

It is important to understand that *when electromagnetic energy of specific wavelength interacts with matter, a characteristic energy response occurs which is specific for that particular kind of matter.*

By means of energy detecting and measuring devices, such as spectroradiometers, spectrophotometers, and precision radiation thermometers, one can determine the energy relationships between specific wavelengths of energy and various kinds of matter. Energy response curves can then be prepared as a function of wavelength. Comparison of these data will reveal the wavelength band (i.e., portion(s) of the electromagnetic spectrum) where the energy response for objects of interest are similar and where they are different. Using this information one can discriminate among significant objects on the resulting remote sensing data by selecting a sensing device which records in the wavelength bands showing greatest energy response difference for those objects. (On the remote sensing records these energy response differences are represented by gray tones, color, or signal output strength.)

In some specific wavelength bands, called "molecular absorption bands," strong absorption by such atmospheric gases as ozone, water vapor, or CO_2 may preclude remote sensing of the earth's surface from aircraft or spacecraft. Also, atmospheric dust and haze particles may preclude sensing in various portions of the electromagnetic spectrum. Haze particles, for example, cause extreme scattering of ultraviolet energy and thus severely limit sensing capabilities in this band. Sensing in the visible spectrum may be precluded by fog, cloud cover, and dense smoke. Thermal infrared energy, however, can be sensed night or day through light fog or dense smoke. Microwave energy can penetrate nearly any weather condition, night or day, thereby permitting radar devices to obtain interpretable imagery.

Thus, an understanding of the complex relationships between energy and matter can permit one to select a remote sensing system for reconnaissance which gathers a maximum amount of information within the environmental constraints placed upon it. (For a more detailed review of basic matter-energy relationships, see Colwell, et al. 1963.)

REMOTE SENSING CARRIER VEHICLES AND DEVICES

Remote sensing began its evolution about 1858, when the first aerial photograph was taken by a camera carried aloft in a gas-filled balloon. Since then, the dirigible, airplane, helicopter, and rocket have carried cameras and other remote sensing devices to obtain photographs and photo-like images from a vantage point above the terrain. The data secured by such systems have been used widely for various military and resource applications. In recent years, photos obtained from manned and unmanned orbiting satellites have demonstrated the potentialities for remote sensing. For example, NASA's Earth Resources Survey Program was established more than 4 years ago to explore the feasibility of developing remote sensing systems for inventorying earth resources from space. This program has stimulated scientists to evaluate all remote sensing devices capable of operating from spacecraft and/or conventional aircraft, and to determine which devices are useful for improving inventories for the various resource disciplines (e.g., agriculture, forestry, range, geology, hydrology, oceanography, geography).

Once the informational requirements have been defined, consideration may then be given to a remote sensing system which permits procurement of data from which interpretations and measurements can yield solutions to resource problems. The information derived from a single remote sensing system in many cases can be used to satisfy a number of different informational requirements of the range or wildlife manager.

Many kinds of remote sensing devices are available for recording information in specific energy bands of the electromagnetic spectrum. Six types of remote sensing equipment show the most promise for inventorying natural resources (Colwell 1968):

(1) The *conventional single-lens aerial* camera. This sensor has a fixed-lens assembly of specified focal length. It collects reflected radiation in the visible and near infrared bands on various kinds and formats of film. Because of the fixed geometry of this system, the resultant photograph provides an ideal map base.

(2) The *panoramic* camera has a movable lens that pivots from a fixed point through an arc and exposes a wide photo swath of the terrain below (perpendicular to the flight line) on a 70-mm. black-and-white or color film emulsion. The panoramic photographs vary in scale from the outer edge into the center of the photo, so although this camera generally is not used for mapping purposes, it can obtain high resolution photographs.

(3) The *multiband* or *multilens* camera is a camera assembly with two or more lenses. By using various filters, several specific bands of energy in the visible or near infrared spectrum can be simultaneously sensed and recorded on film. In some instances several film types are exposed simultaneously through a multilens camera.

(4) The *optical mechanical scanner* can record energy responses in the ultraviolet, visible, near infrared, and far infrared bands simultaneously by using a variety of detectors sensitive to radiation of different wavelengths. Unlike a camera, the scanner focuses reflected and emitted radiation through mirrors onto sensitized detectors by means of a rotating prism. The energy response received by the detectors (photo multiplier tubes for the visible and near infrared and solid state semiconductors for the thermal infrared), is converted into electrical impulses, which are either recorded on magnetic tape or are converted by means of a cathode ray tube into a series of line scans that form a continuous photo-like image of the terrain below. (The term "imagery" refers to the photo-like presentation of line scan data.)

(5) *Side-looking radar* is an active all-weather sensing system that generates its own long-wave radiation, transmitting it to the terrain below. The returning radar impulses are received via an antenna and transformed through several steps into photo-like images, usually in the form of contiguous line scans.

(6) The *gamma ray spectrometer,* which can only operate at a short distance above the terrain (due to atmospheric absorption) to record gamma rays emitted from radioactive materials. Very little application of the gamma ray spectrometer is expected in range environments, except for mineral exploration.

A brief description of the operating characteristics of these sensing devices is given by Colwell (1968).

Cameras, Films, and Filters

Much of the early panchromatic photography was obtained with a *T-11 mapping camera* and a *K-17 reconnaissance camera.* Both meet the minimum standards for mapping vegetation and soil; hence, they have been greatly used for this important application. The types

of aerial cameras known to be in use as of 1965 and the principal specifications and characteristics of each type are given by the American Society of Photogrammetry (1966).

Higher resolution mapping frame cameras —e.g. *Zeiss RMK–A15-/23* and *Wild RC-8, RC-9*—have been used to obtain experimental photography of rangelands with different films and scales (1/4,000 up to 1/85,000).

A Maurer KB-8, 70-mm. camera system capable of obtaining very large scale photographs, can be an extremely useful tool for improving range resource analysis (Carneggie 1968; Reppert and Driscoll conference paper). Rapid shutter speeds and film advance rates allow this camera to be operated at altitudes as low as 300 feet. The resulting large-scale photography, 1/600, can be used to detect and to identify objects as small as 1 to 2 inches. Recognized applications of these photos include: (1) Identification of range plants (by species), plant conditions (e.g., health, leafiness, and utilization) and soil surface phenomena (e.g., rockiness, erosion, disturbance by grazing animals, rodent activity, and animal droppings); and (2) quantification, either by estimate or direct photo measurement, of vegetation paramenters such as plant cover, density, and height. Examples of large-scale color and color infrared photos appear in figures 2 and 3 (color plates I and II) and illustrate the tremendous capability of this camera system for gathering information.

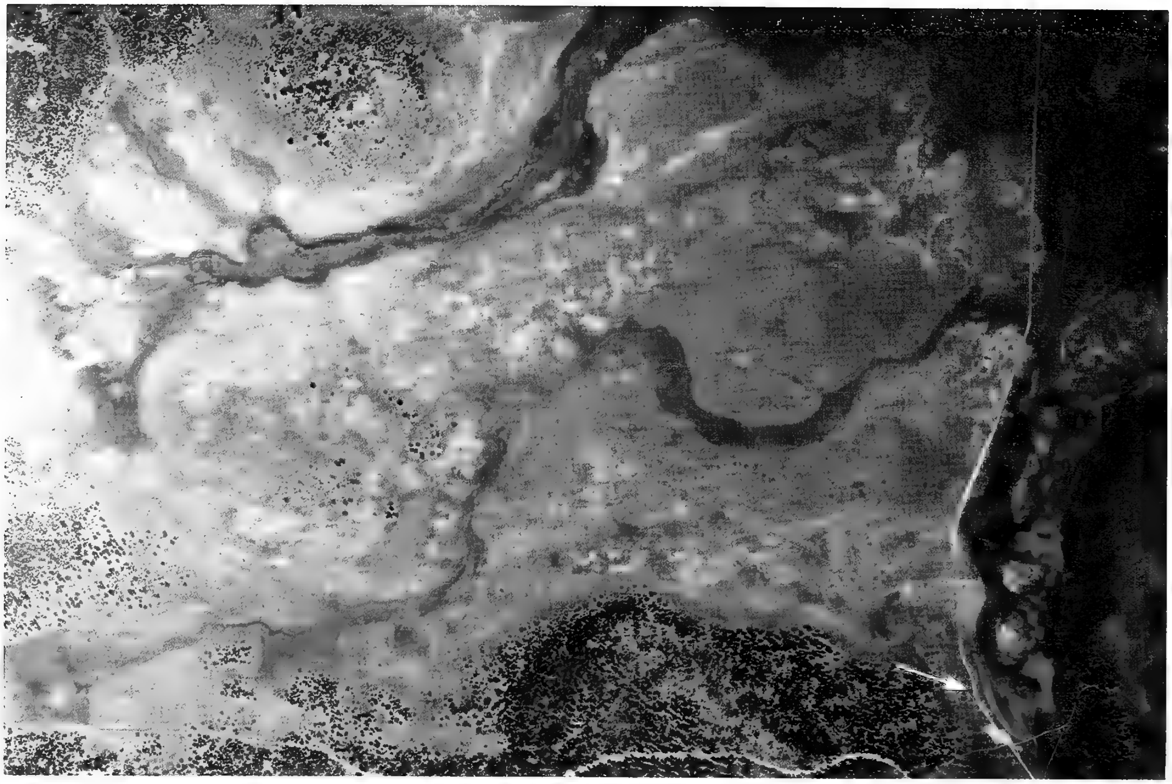
Animal inventory, assessment of factors influencing productive capacity, detailed mapping, and analysis of innumerable management problems are among the many ways information can be utilized. However, because the aerial coverage per exposure is relatively small (14,400 sq. ft. at a scale of 1/600), the greatest potential of this system will no doubt be realized when it is used in conjunction with small-scale or low-resolution systems to provide a detailed picture of selected "key" (sample) areas. The information derived from direct interpretation and measurement on the large-scale photos combined with limited ground study can then be applied over a much larger range area, thereby improving the accuracy of interpretations made from small-scale, low-resolution systems (operating at a high altitude or from earth orbit). As an example, livestock counts made from panchromatic photos (1/5,000) were more accurate when large-scale (1/2,140) 70-mm. color transparencies were simultaneously obtained to subsample a small area contained on the panchromatic photo (Huddleston and Roberts 1968).

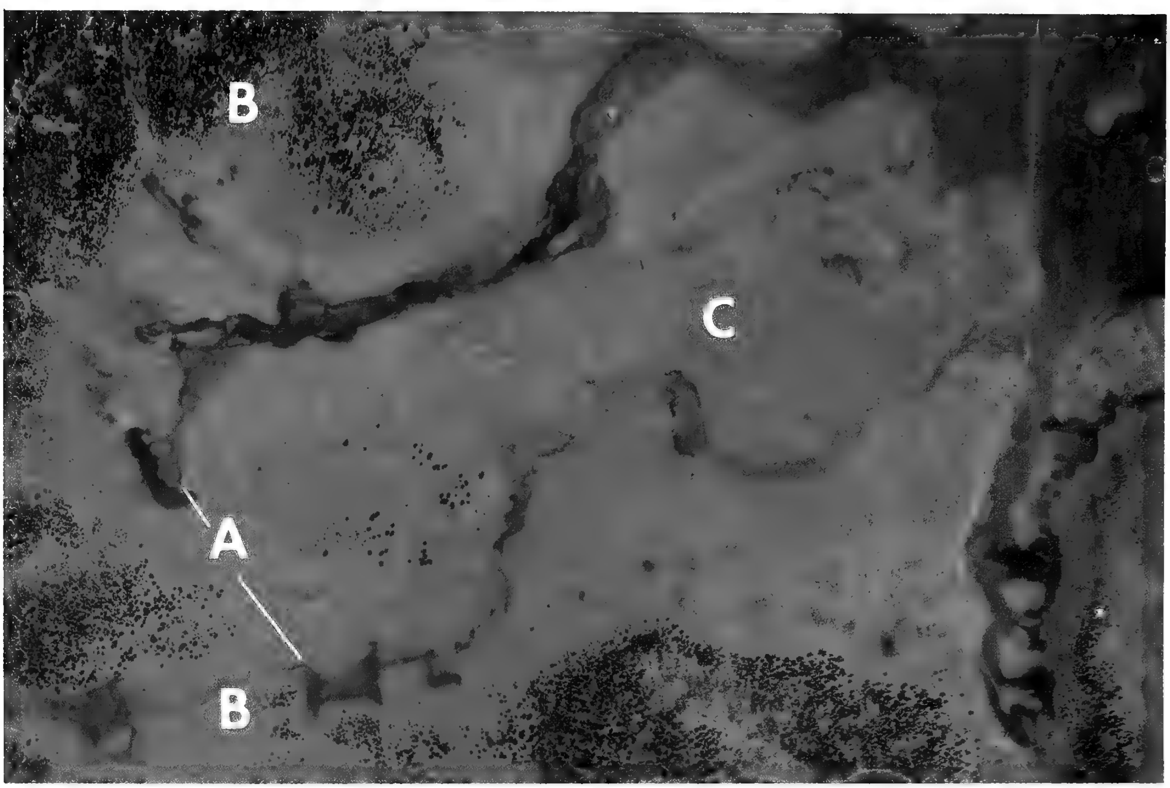
Multiband photographs obtained with a four-lens multiband camera are illustrated in Figure 4. Note that two film types—panchromatic and near infrared—were exposed simultaneously through four filters to give four narrow band photographs. Such a system theoretically allows the interpreter to discern more features. That is, the multiple photographs accentuate vegetation-soil boundaries by exploiting unique tone signatures in various portions of the visible and near infrared spectrum. Unfortunately, interpretation of this photography is tedious and time consuming unless facilities are available to reconstitute the black-and-white images into a single color composite. (A relatively new interpretation technique known as image enhancement by additive color reconstitution has been developed). Researchers believe that multilens cameras can be effectively operated from space platforms because a higher resolution image can be obtained using black-and-white film. Only limited use of the multilens camera, e.g., for special-purpose inventory, is anticipated for conventional range analysis.

Panchromatic, Aerographic Infrared, Aerial Ektachrome, and Ektachrome Infrared Aero (color infrared) aerial photographs have been compared to determine the ease and accuracy of extracting information from them for improved resource analysis (Carneggie et al. 1966, Carneggie, et al. 1967).

Panchromatic film emulsions (figure 5) are sensitive to visible radiation from 0.4 to 0.7 micron. However, panchromatic film is frequently exposed with a minus blue (Wratten 12) filter to reduce scattering effects due to haze. Occasionally a red filter (Wratten 25A) is used to improve tone contrast between vegetation and soil. The various gray tones seen on

FIGURE 2 (Color Plate I). Part of Harvey Valley Range Allotment, Lassen National Forest, northeastern California is shown on Ektachrome Aerographic (top) and Ektachrome Infrared Aero (color infrared—bottom) aerial photographs. This perennial bunchgrass-sagebrush range was photographed on June 11, 1966, at a scale approximating 1/28,000. The original 9 by 9 inch transparencies cover a range area of approximately 16 square miles. The Ektachrome Aerographic photo gives a more representative picture of vegetation-soil color. However, notice the unique color renditions and contrasts in the Ektachrome Infrared Aero photo; these are particularly useful for detecting and for estimating the cover of range vegetation. For the purpose of identifying some important range types, meadow vegetation is indicated at A, a Big Sagebrush community is indicated at B, and dense native perennial grass is indicated at C. A very large-scale photo showing the sharp ecotone indicated by the arrow is seen in figure 3 (color plate II).

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the panchromatic photo image indicate the amount of visible radiation which is reflected from features on the ground. Dark tones on the positive print indicate objects having low reflectance, while light tones indicate those of high reflectance.

The *Aerographic Infrared film* emulsion (figure 5) when exposed with a Wratten 89B filter records only near infrared wavelengths of light (0.7 to 0.9 micron), i.e., wavelengths of radiation just beyond what the human eye can see. Since healthy vegetation exhibits high infrared reflectance, it appears light in tone. Soil generally has relatively low infrared reflectance and appears dark in tone (see figure 5). The tone contrast between healthy vegetation and soil in the near infrared portion of the spectrum is particularly significant since range managers are concerned about the presence and amount of range vegetation.

Aerial Ektachrome film is a three-layered emulsion sensitive to blue, green, and red wavelengths of light (see figure 2). When they are processed, the activated dyes combine to form colors which may closely match those of the original scene. True color rendition is difficult to obtain, and it is especially difficult to replicate from one photo mission to another due to variations in processing, exposure, and spectral reflectances of the objects as well as the sensitivity of the emulsion base. Despite these problems, considerable refinement in mapping and interpretation can be expected compared to black-and-white photographs.

Ektachrome Infrared Aero film is a three-layered emulsion sensitive to green, red, and near infrared wavelengths of light which activate yellow, magenta, and cyan dyes, respectively. When processed to a positive image, the resulting colors in the photograph are blue, green and red, respectively (Fritz, 1967). A Wratten 12 or 15 filter is generally used when exposing this film to omit blue wavelengths of light, to which all three layers of this film are also sensitive. On color infrared photographs, healthy vegetation—which has relatively low reflectance in the visible portion of the spectrum (except in the green region) and relatively high reflectance in the near infrared—appears reddish; hence, healthy vegetation is readily detected (see figure 2). Color infrared film can be used to record many plant conditions because the intensity of near infrared radiation reflected from healthy vegetation is a function of the quantity and compactness of green foliage, the moisture content of the leaves (Weber *et al.* 1967), the phenological development of foliage, the disease status of the foliage (Colwell 1956), and plant cell anatomy. Bare soil, which normally appears reddish or brownish, appears greenish on this film.

Detailed photo interpretation of both annual and perennial rangeland on 9- by 9-inch film format, at scales between 1/8,500 and 1/85,000, indicate that panchromatic photos are adequate for delineating broad vegetation and soil boundaries. The level of detail in mapping depends upon photo quality; the scale of the photos; and the interpreter's skill in discriminating tone, texture, shape, size, etc., of significant features.

Aerographic infrared photos conspicuously show meadows and other dense vegetation types. A variety of moisture regimes, e.g., streams, ponds, and standing water, are also easily detected; however, such photos are not considered useful for general vegetation-soil mapping in rangeland.

Color photographs (both Ektachrome and Ektachrome Infrared) permit considerable refinement in mapping accuracy. We would expect this gain because the human eye can discriminate far more shades of color than shades of gray. Aerial Ektachrome photographs are particularly useful for soil boundary delineation where range vegetation is sparse or when obvious changes in vegetation type correspond to changes in soil type. By using soil color characteristics to identify soil types, other related information, such as soil fertility and associated vegetation, can be inferred. Whereas meadow vegetation usually can be identified on the color photos, other important range vegetation types with sparser foliage cover are not as readily discriminated, due to a lack of sharp color contrast between vegetation and soil. This problem becomes more noticeable on smaller scale color photography.

Ektachrome Infrared Aero photos appear to be the most easily interpreted for detection, identification, and evaluation or mapping of vegetation-soil boundaries, changes in vegetation density, and moisture regimes, e.g., wet meadows sustained by subsurface and surface spring water flow, and marshy conditions formed by standing spring water (figure 2). Likewise, detection and identification of management problems are also facilitated by the *unique color renditions* and *increased contrasts* produced on the color infrared film. However, many ranges, particularly xeric ranges, may not contain a variety of conditions which are best discriminated on Ektachrome Infrared Aero film. Hence, another film type, e.g., panchromatic, may be just as useful for inventory purposes.

Before indiscriminately procuring photos for inventory purposes, one should consider these factors: (a) The diversity of physical and biological characteristics (complex vegetation-soil-moisture regimes are more interpretable

on color and false color photos); (b) The level of information desired (color photos provide considerable refinement in mapping, and large-scale photos show greater ground detail), and (c) The cost differential between black-and-white and color photos (color photos are generally two to three times greater in cost per exposure). Final consideration should also be given to the tradeoff between choice of film type, cost per exposure, and scale of photography.

As an example, in some range environments the increased information derived from interpretation of color infrared photos (compared to panchromatic) may permit procurement of smaller scale photography (e.g., 1/30,000) which covers a larger range area. Thus, the fewer color exposures required may offset the additional cost per exposure and bring the total inventory cost in line with the cost of procuring black-and-white photos taken at a relatively larger scale (1/15,000 to 1/20,000).

Line Scan Devices

The use and interpretation of line scan imagery from an *optical mechanical scanner* is still in experimental stages. Figure 6 shows 5 of 18 spectral bands which record both reflected and emitted radiation in the ultraviolet, visible, near infrared, and thermal infrared portions of the electromagnetic spectrum. By comparing the tone signatures of the various range features illustrated, one can see that the energy responses from bands of the spectrum are very different. Some range features are emphasized on one band but are obscured on another band. Consequently, it is most desirable to interpret the band(s) which reveal the greatest information about the features of particular interest. For example, an image obtained in the visible band of the spectrum is better for delineating the most vegetation and soil boundaries, whereas significant moisture regimes are emphasized on the thermal infrared image.

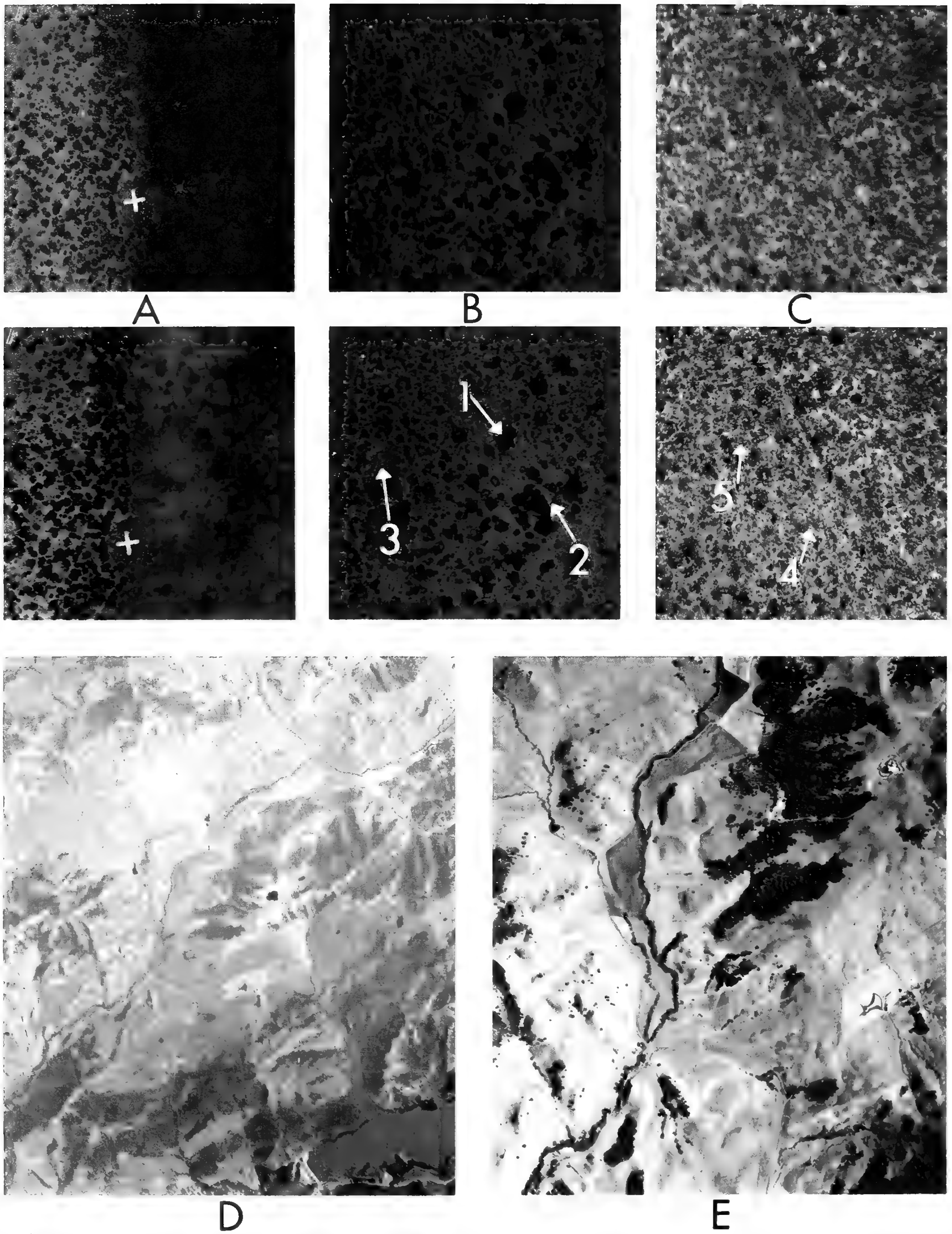
Advantages of the optical mechanical scanner over photographic systems previously discussed are: (1) Imagery can be generated simultaneously in wavelengths both within and outside the photographic region; (2) the signal is in an electronic form and can be stored on magnetic tape or converted to a photolike image; and (3) the detectors generally have a wide dynamic range and hence more tone values can be discerned. On the other hand, limitations of the scanner are: (1) It is more complex than a camera; (2) it generally has poorer spatial resolution than a camera; and (3) it has distortions which are difficult to eliminate or rectify (Lowe 1968).

Thermal infrared imagery of perennial rangelands in northeastern California, has been obtained with a *Reconofax IV infrared imager* (see figure 7). Dark tones within the image indicate low emitted radiance associated with low temperatures, whereas light tones indicate high emitted radiance associated with features which are warm. This day-or-night sensing device provides a capability for discriminating objects having different thermal emission (temperature emissivity). Applications suggested by the thermal infrared image in figure 7 include detection of springs and differentiation of water temperatures. Other applications of thermal infrared imagery which seem feasible are: (a) Monitoring moisture regimes before, during, and after the grazing season; (b) determining range readiness and availability of stock water for efficient range management; (c) detecting moisture regimes which aid in analyzing the presence or distribution of important vegetation types; and (d) inventorying of domestic or wild animals. Resolution constraints presently limit operation of infrared imagers to relatively low altitudes, but even so, the feasibility for detecting animals in the open, i.e., not beneath a vegetation cover, has been demonstrated (Garvin et al. 1964; Carneggie et al. 1966, 1967).

Side-looking radar devices have been operated over rangeland in Oregon, California, Utah, and Kansas. Analysis of radar imagery for vegetation studies is summarized by Moore and Simonett (1967). Their results indicate that radar may have a role in preparation of small-scale regional or reconnaissance vegetation maps, particularly where there are pronounced structural differences between plant communities. Although the resolution of radar imagery is generally much lower than that of photographs taken at the same altitude, the ability of radar devices to obtain imagery day or night, and during most adverse weather conditions, makes it a promising sensor for a special-purpose inventory—for example, in range environments characterized by persistent cloud cover which would prevent the attainment of photographs. There is also evidence that longer wavelength radar pulses, capable of penetrating soil to various depths, may be extremely useful for analysis of soil properties.

REMOTE SENSING DATA ANALYSIS

Analysis of most remote sensing data depends primarily upon recognition of the energy responses (associated with reflectance or emittance of radiation) from objects in the various portions of the electromagnetic spectrum. Through procurement and analysis of many kinds of remote sensing imagery, such as have been presented in this paper, an image analyst soon becomes familiar with tone or color re-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sponses associated with significant range phenomena. Also, he uses other image characteristics, including size, shape, texture, pattern, and associated features, to aid in detecting, identifying, and evaluating directly, or by convergence of evidence, most discernible features. Ultimately, the image analyst can check the accuracy of his interpretations by either (a) comparing them with ground information obtained at the time of the overflight, or (b) by taking the remote sensing data into the field and comparing it with ground features.

These "tried and true" visual interpretation techniques for extracting information from an image are well established and are adequate for analysis of relatively small land areas. (A complete treatment of photo interpretation may be found in "Manual of Photographic Interpretation" (American Society of Photogrammetry 1960).

However, for analysis of large areas where the need for rapid and detailed information is urgent, image interpretation using visual techniques may be too time consuming.

A means for increasing the rate and accuracy of information extraction from remote sensing data—using visual interpretation—is by a double-sampling procedure. Such a procedure involves procurement of imagery of an area from two levels. For example, a generalized, synoptic view of a large land area can be provided by high-flying aircraft, or from earth-orbiting vehicles. At the same time, a very detailed view of small sample sites within such a large area could be obtained using a 70-mm. camera system capable of procuring large-scale photos. Thus, an image analyst could derive detailed information by studying a few images of sample sites and extending this information over a much larger land area as provided by the synoptic view.

To satisfy the increased demand for rapid information about our resources, the day may come when several remote sensors will be operated at frequent intervals (as from an earth-orbiting vehicle.) Then, the photo interpreter left to his own means may suddenly become deluged with remote sensing data. Recognition of this problem has spurred research efforts for more rapid techniques for extracting information from the remote sensing data.

The photo interpreter's judgment is not likely to be replaced by automation, but many encouraging techniques yet in the rudimentary stages have been recognized as being capable of assisting him and expediting information flow (Colwell 1968):

(1) *Image enhancement by additive color techniques* (described in detail by Yost and Wenderoth 1968). Briefly, this technique permits an interpreter to analyze simultaneously many black-and-white images such as those in figures 4 and 6. The black-and-white images theoretically having the same geometry are projected through various colored filters and are superimposed in common registry on a screen. A single color composite formed in this manner brings together in various colors the tone signatures unique to many spectral bands.

FIGURE 3 (Color Plate II). Photo pairs, A, B, and C (corresponding Anscochrome color and Ektachrome Infrared Aero photos) show enlarged portions of large-scale 70-mm. aerial photographs. Photo pair A, taken in July, shows a sharp ecotone between a big-sagebrush and wet meadow plant community (the small-scale view is seen at the arrow in color plate I). At this large-scale (= 1/600) one can estimate shrub density and cover. Cattle droppings can be discerned in the meadow. Note also the rodent paths in the meadow. Photo pair B, taken in July, illustrates the feasibility of identifying range plants. Bitterbrush (*Purshia tridentata*) at *1* (a palatable species for cattle and deer) is readily distinguished from big-sagebrush (*Artemisia tridentata*) at *2* (important because of its abundance, but not a preferred species by either cattle or deer) on the Ektachrome Infrared Aero photo. Buckwheat plants (*Eriogonum* sp.), are readily identified at this phenological stage by yellow flowers, at *3*. Photo pair C, taken in late August, shows range vegetation in the Black Mesa area of Colorado. *Helenium hoopseii* at 4 and *Geranium fremontii* at 5 are distinguishable from other species on the Ektachrome Infrared photo; this again illustrates the feasibility of identifying important range plants at the appropriate phenological stage (see text by Reppert and Driscoll in these Proceedings for further detail).

Photo D is an Ektachrome Infrared photo taken in early May 1967, with an RC–9 camera (scale 1/84,000); California annual grassland, east of Berkeley, Calif., is shown. At this date, the dense, healthy range vegetation associated with deeper soils appears reddish, whereas the range vegetation associated with shallow upland sites and south-facing exposures has dried and appears straw colored. Variations in the reddish appearance of the healthy annual grass may be attributed to species composition, vegetation density, degree of utilization, and vigor or health.

Photo E is also an Ektachrome Infrared Aero photo which shows a portion of the same annual grassland seen in photo D, but at a relatively larger scale, 1/33,500) and at a different seasonal stage (August). Observe that in August when all the annual vegetation is dry, there is little advantage to using color infrared photos to evaluate range conditions.

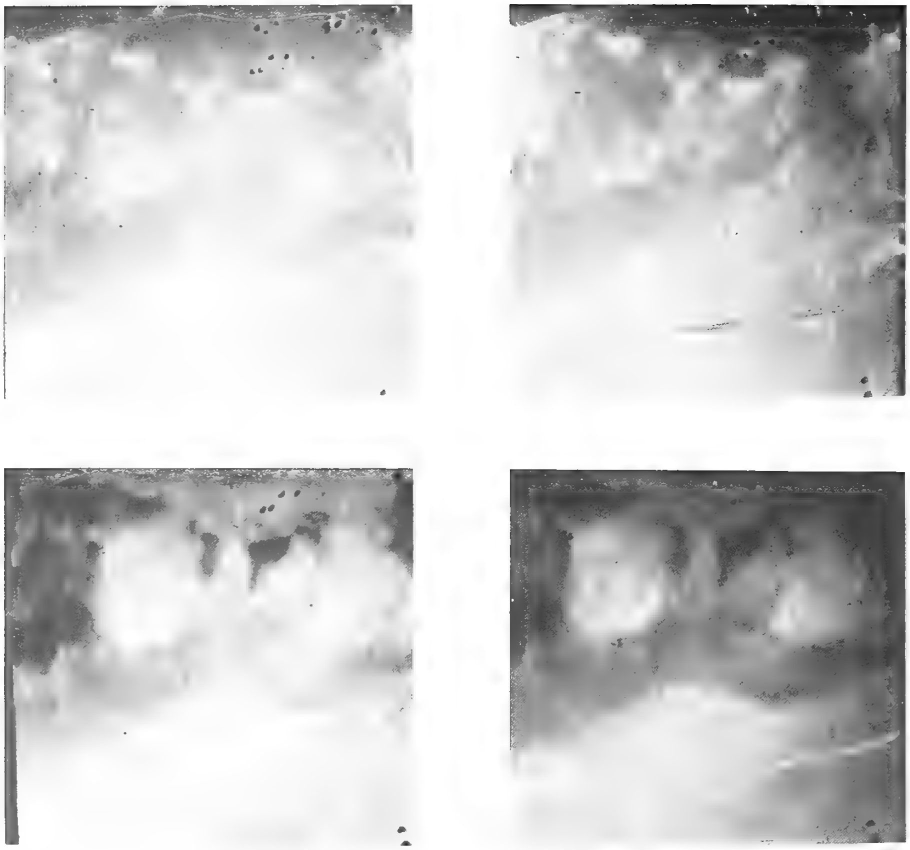

FIGURE 4. These four photos were taken simultaneously with a 4-lens spectraband camera system. The photos above are: Upper left, Plus-X panchromatic with a Wratten 25A filter (0.6–0.72 micron); upper right, Plus-X panchromatic with a Wratten 61 filter (0.46–0.61 micron); lower left, Infrared Aerographic with a Wratten 47B filter (0.35–0.50 and 0.72–0.95 micron); and lower right, Infrared Aerographic with a Wratten 89B filter (0.72–0.95 micron). Tone differences for range features seen here may be either quite pronounced or quite subtle, depending upon the narrow spectral bands which are compared. Interpretation of these images can be facilitated by additive color enhancement techniques, whereby a single-color composite image is made by superimposing two or more black-and-white images, such as those above, with various colored filters.

(2) *Photoelectric scanning of black-and-white images.* In this technique, the black-and-white images are automatically scanned to determine tone signatures for objects in the scene. Each signature is characterized by a coded symbol. The digitized printout is then automatically processed to determine the kind and quantity of objects in the original image.

(3) *Automatic tone signature recognition* using a computer (Laboratory for Agricultural Remote Sensing, Purdue University 1967.) This process, designed primarily to analyze many channels of optical-mechanical scanner data, involves recording energy responses on magnetic tape. The computer then compares the energy response from the magnetic tape with known energy responses for previously identified agricultural crops. The matching of these signatures by the computer permits rapid crop identification.

OUTLOOK AND SUMMARY

It should be evident from this review that remote sensing offers great potential for gathering information for range and wildlife inventory and management. However, if its full potential is to be realized, range and wildlife managers must understand matter-energy relationships, sensor limitations and capabilities, factors which either limit or enhance image interpretability, applications, and benefits. Managers should also be aware that a great gap currently exists between the capability for gathering a large amount of remote sensing data in many portions of the electromagnetic spectrum and the limited capability for handling and analyzing it (Lent and Thorley 1968). Furthermore, the average user may become overwhelmed by the expense and sophistication of certain remote sensing systems. He

then sees little relationship between his problem and the practical application of a complicated array of sensors, and he concludes that assist him with his inventory problem. However, remote sensing research can equip the remote sensing is far too complex and costly to range and wildlife manager with a knowledge of remote sensing problems as well as potentialities, so that he can better understand where, when, and how remote sensing can be used effectively as a tool for resource inventory and management. In addition, the user ought not assume that any one management activity will have to bear the cost of the whole system, for the benefits of remote sensing to the forester, agriculturist, hydrologist, geologist, and recreation planner also appear large indeed.

FIGURE 5.—These two aerial photographs of Harvey Valley Range, Lassen National Forest, Calif., show the different energy responses of range features in two bands of the electromagnetic spectrum. Notice the ease of detecting meadow vegetation at *A*, standing water from a spring at *B*, low sagebrush type at *C*, and other vegetation-soil boundaries at *D*. Also compare this range area with the corresponding range area as seen in color plate I, and figures 4, 6, and 7. The top photo was obtained with Plus-X Aerographic film (type 2401) with a minus-blue filter (0.5–0.7 microns). The bottom photo was obtained with Infrared Aerographic film (Type 5424) with an 89B filter (0.7–0.9 microns).

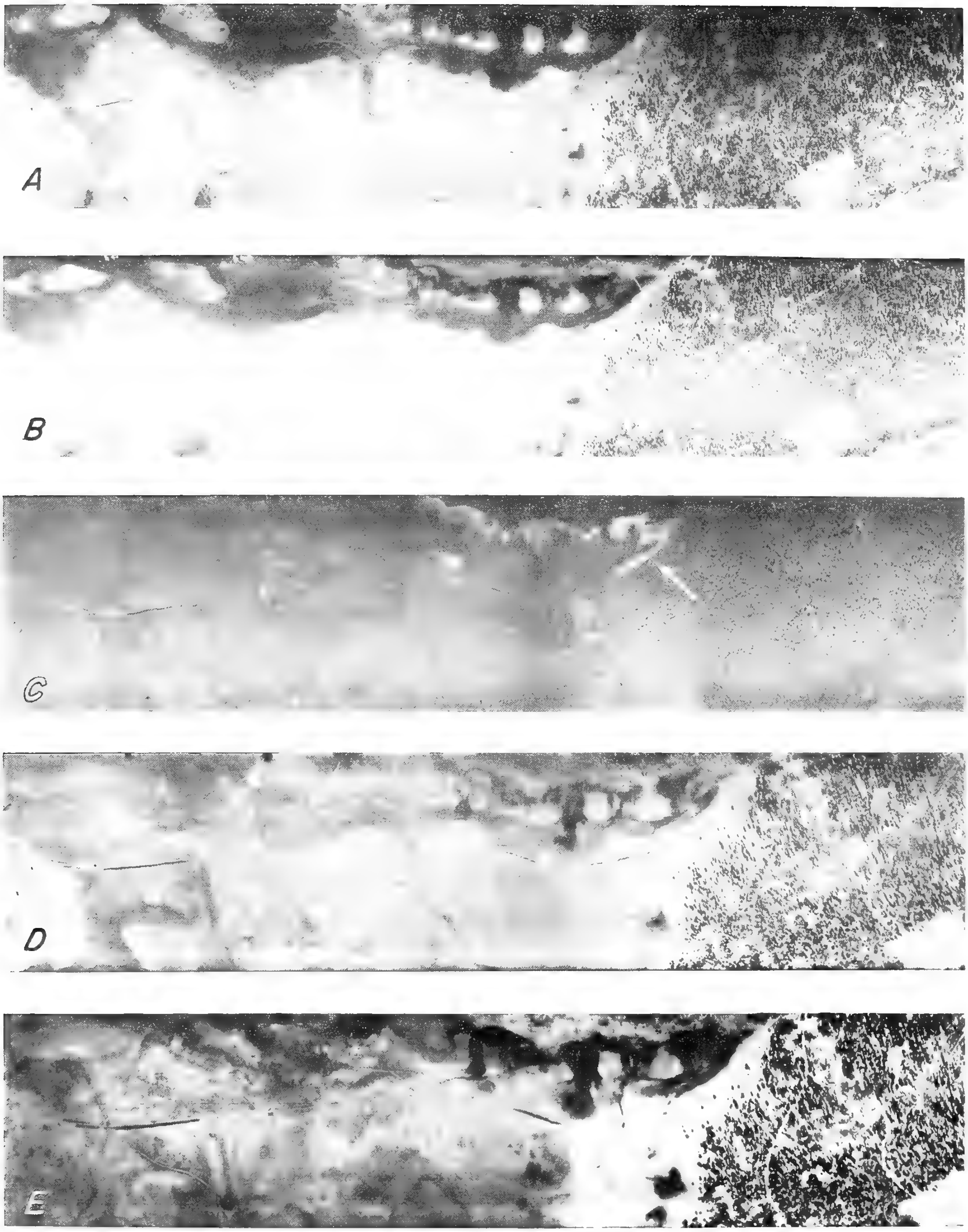

FIGURE 6. Line-scan imagery obtained by an optical mechanical scanner. The five spectral bands shown here were among 18 bands which can be recorded simultaneously. A is an ultraviolet image (0.32–0.38 micron); B is a visible-red image (0.62–0.68 micron); C is a near-infrared image (0.80–1.0 micron); D is also a near-infrared image (1.5–1.8 micron); and E is a thermal infrared image (8.0–14.0 micron). Notice the different tones of features in the different parts of the electromagnetic spectrum. Notice also that certain range features are seen more readily in one band than in another. The visible band shows the most vegetation-soil boundaries. The near-infrared band (0.8–1.0 micron) shows dense meadow vegetation most clearly. The other near-infrared band (1.5–1.8 micron) emphasizes standing water, and the thermal infrared band shows temperature differences due to moisture effects, vegetation density, and soil surface characteristics.

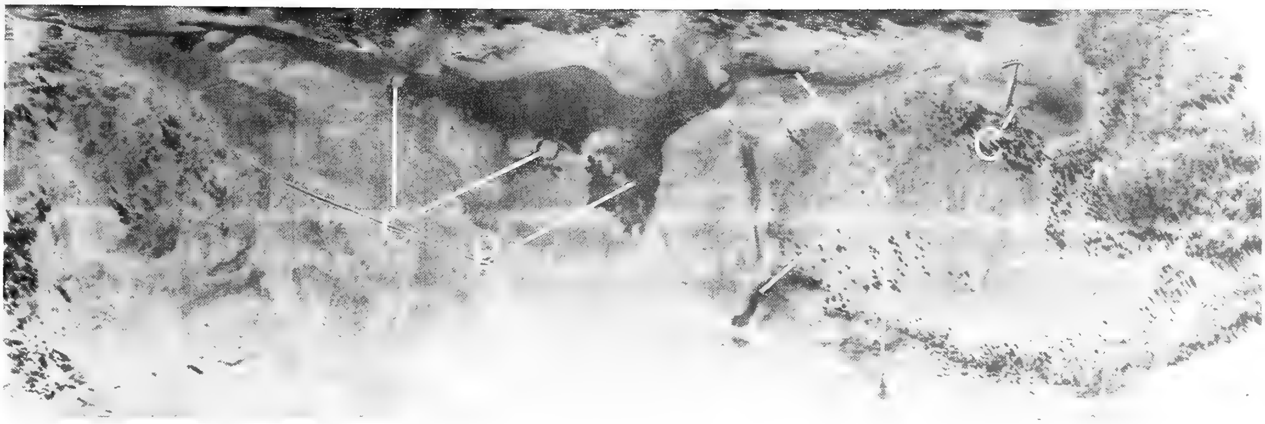

FIGURE 7.—Line scan thermal infrared imagery. The top image, taken with an airborne sensor during the late morning, shows a portion of the Harvey Valley Range in a late fall stage (October). Vegetation-soil boundaries are not readily seen at this time, but springs (at *A*), spring water (at *B*) and ponded water which is warmer than the spring water (at *C*), are clearly seen. Livestock, both sheep (at *s*) and cattle (at *c*), are seen on the bottom thermal infrared image taken with a ground-based camera from atop a 150-foot water tower at 11 p.m.

Already, many useful applications of remote sensing are recognized, and even more potential applications are visualized. But before new remote sensing techniques can be accepted, they must be justified by the time and expenditures saved and by the improved information that is provided. Since most new remote sensing techniques have not yet been employed in operational surveys, the applications and benefits to accrue remain a matter of much optimistic speculation. As usual, more research is required.

A problem-oriented approach is needed to define meaningful problems for which remote sensing applications promise to provide benefits, and to establish priorities for testing them under experimental and operational conditions. At the same time, we cannot overlook the opportunity to continue experimenting with present and newly developing sensors, for this kind of investigation will uncover new applications.

Furthermore, we must recognize the importance of gathering good ground information at the time of the overflights if we are to make meaningful interpretations from the remote sensing data. For without detailed records of plant, soil, and moisture conditions at the time the remote sensing data is procured, an interpreter cannot determine the accuracy of his interpretations. This paper does not discuss techniques for collecting and analyzing ground information; however, the importance of this aspect of remote sensing cannot be overemphasized. Finally, before remote sensing techniques can be applied operationally, we must develop a program of remote sensing education for range and wildlife specialists so that when

remote sensing data are available, they can take it or the information derived from it into the field to aid in solving inventory and management problems.

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Practical Applications of Remote Sensing in Range Resources Development and Management

CHARLES E. POULTON[1]

INTRODUCTION

Since 1962 some of my colleagues, graduate students, and I have been engaged in a research program at Oregon State University aimed primarily at the ecological analysis of range resources.

The purpose of this paper is to present some of the more practical aspects of what we have learned from our work with conventional black and white aircraft photography as an aid to the decision process in the multiple use and management of these resource areas. Many of the ideas will also be applicable when using the output from all photographic systems and from many of the more sophisticated developments of the space age.

WHY REMOTE SENSING OF RANGE RESOURCES–

If we are to capitalize on the full capability of remote sensing as a day-to-day working tool in the range resources area, it will be worthwhile to place the range in perspective with other related natural resources upon which human society depends. Before civilized man came on the scene, all food and fiber resources on the earth could be classed as range or forest except for those existing in water of the earth (fig. 1). From these naturally vegetated resource areas, man has carved his agricultural cropland—tending always to take the best land first. Around these croplands he has built his cities, industries, and transportation facilities and superimposed his social, economic, and political cultures. From the beginning of recorded time, ranges or native pastures have been an important contributor to, and component of, this culture.

Remote sensing and ecology must both be considered to provide the high-level decision makers in our society with the required understanding—or with the capability to efficiently acquire an understanding—of the resource.

Ecological research, particularly in phytosociology and vegetation-soil relationships, provides an understanding of the resource that is required for multiple use management of naturally vegetated areas. Phytosociological classification of plant communities is essential to

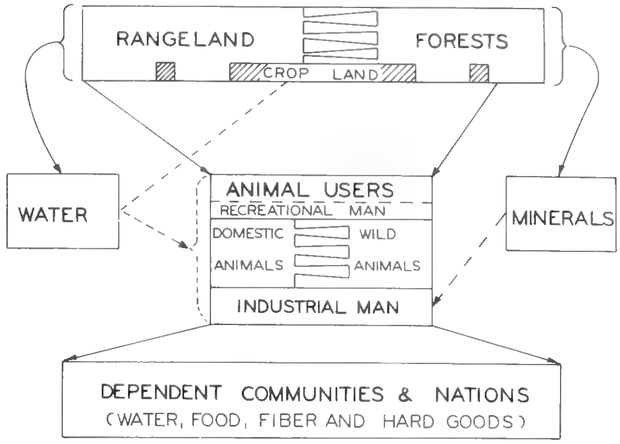

FIGURE 1.—Dependence of human culture on naturally vegetated resource areas and product flow lines from resource to society.

permit the most meaningful interpretation of photo images in range and forest resource analysis. These classifications provide the basis for legend development in ecological resource analysis. Full development of photo interpretation capability provides the most efficient mechanism for applying this ecological knowledge to the land in the determination and mapping of site characteristics, potentials, and limitations. Therefore, the primary purpose of remote sensing in the ecological analysis of range and related resource areas is (1) to increase efficiency and minimize cost of resource analysis for multiple use management and (2) to minimize, but not replace, fieldwork in the acquisition and mapping of information to meet these management-oriented needs.

Ecological resource analysis, achieved through optimum use of remote sensing, provides the best possible base upon which to accumulate data relevant to land uses and problems. It provides the only universal and biologically sound concept of site upon which to generalize or extend the results from research and successful management practices.

To achieve the full spectrum of benefits from range resources throughout our country, and in the various nations of the world, more complete and ecologically accurate information about the resource is needed in different forms and levels of detail for policy, land use planning, and resource management decisions (fig. 2).

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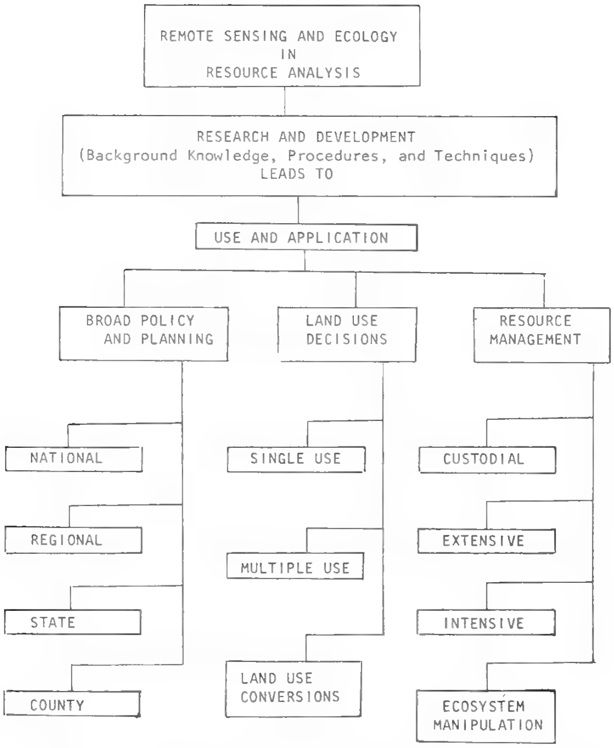

FIGURE 2.—The functions and levels of activity within the scope of natural resource use that are served by remote sensing. Each function and level has its unique requirements.

Each level, from broad policy planning to decision monitoring, has a unique requirement for remote sensing systems and output, ecological interpretations, and information summaries. At each level, particular photo image interpretation problems unique for that information level are encountered. For example, at the decision-monitoring level, the need is for unusually large-scale photography, with interpretation emphasis on individual species and photogrammetric measurement as illustrated by conference papers of Driscoll and Reppert.

Photography taken from space platforms may be especially valuable for making broad national and regional policy decisions. In this instance, photo interpretation draws much less strongly on the textural characteristics of the image and instead emphasizes color or tones, gross patterns, and convergent or associated evidence in making judgments from the photography. In addition, photo interpretation of extremely small-scale photography emphasizes ecologically similar groups of plant communities rather than the individual species. The specific plant communities are emphasized in the interpretation of photography taken at conventional scales for resource management purposes. In all the levels illustrated in figure 2, remote sensing and photo or image interpretation is destined to play a rapidly increasing and valuable role.

BACKGROUND ON THE USE OF REMOTE SENSING IN RANGE RESOURCE ANALYSIS

The first range survey in the United States was conducted entirely by ground methods on the Coconino National Forest, Ariz., in 1911. From that year until the beginning of World War II, methods were changed and improved somewhat, but the process remained essentially an on-the-ground technique. In many instances, the need to obtain information on range resources preceded the availability of any kind of planimetric map. In these cases, surveys were conducted by traversing compass lines across the landscape and sketching in the planimetric detail. At the same time, type mapping was done and data were gathered on the resource and its management problems.

In 1935 and 1936 (Moyer 1950) black-and-white aerial photography at the common scale of 1:20,000 became available to range resource people in limited areas.

Unfortunately, about this same time a number of factors were operating to slow progress in aerial photography of rangelands. In the 1930's rangeland was still priced at $2.50-$3.00 per acre, and people generally felt that one could not justify spending money on such "cheap land," especially not for aerial photography.

In concluding their studies, which began in 1939, on the comparative merits of using aerial photos vs. other mapping techniques in range survey, Reid et al. (1942) stated that aerial photography taken especially for use on range survey could not be economically justified. This conclusion was reached by considering only the increase in statistical accuracy of estimates of grazing capacity that resulted from use of photography as a mapping base. In those years, more benefits and cost reductions could have resulted from application of the then embryonic field of photo interpretation.

While Reid et al. (1942) were talking about 7.98 mills more cost per acre and 17 to 20 mills of total cost (including photography), their view was shared by many in responsible administrative positions. This common attitude had such an impact that range resource analysts and managers have mostly been forced to use photography taken and printed to specifications developed for other disciplines and purposes than looking at shrub, grassland, forest opening, and forest understory vegetation. This has made our work with aerial photography difficult and frustrating; it has also prevented range resource people from developing

the full, modern capability of aerial photo interpretation as a tool in their day-to-day work.

Despite the slow rate at which good aerial photography has become available to range managers, in the late 1930's and early 1940's they were among the first to use aerial photography in resource surveys. Range technicians quickly found that they could: (1) Do more consistent and accurate mapping of resource characteristics, (2) estimate parameters for sampling more precisely, and (3) perform necessary fieldwork more efficiently (Reid et al. 1942, Clouston 1950). Aerial photography was found so superior to the grid-traverse, planimetric, topographic, and formline mapping methods used in range surveys through the 1930's that small-scale Army Mapping Service photography was used where nothing better was available. Henriques (1949) has written of the advantages of controlled mosaics for range resource mapping and of the substantial use of aerial photos in regular range management within the Bureau of Land Management starting immediately after World War II.

The Soil Conservation Service, U.S. Department of Agriculture, has used aerial photographs to make range site and condition surveys since they became available to the Department in the mid-1930's. The Soil Conservation Service also pioneered in the use of uncontrolled photo mosaics at scales as large as 1:15,840 in the cartographic presentation of range site and condition survey information and the details of the management program. Similarly, the Bureau of Indian Affairs, U.S. Department of the Interior, has used aerial photography to make some combined range and soil surveys on Indian lands. The Pacific Southwest Forest and Range Experiment Station, through the California Soil-Vegetation Survey Program, has advanced the use of aerial photo interpretation in the field mapping of both vegetation and soil features of range and forest areas. With very few exceptions, all of this work has been done with aerial photography taken for some purpose other than range resource analysis.

Even though more than 90 percent of the agricultural land had been photographed by the beginning of World War II, rangeland generally was only photographed to block out flightlines near cropland. It was not until the late 1950's that aerial photography, other than very small-scale Army Mapping Service photos, became generally available for the western range. It may surprise some individuals to learn that first-time coverage is still being flown over important range areas at scales acceptable for intensive range resource analysis and management (1:15,840 and 1:12,000).

Largely because of variation in the quality of photographic prints and season of photography, range management people have done little to develop photo interpretation aids and keys that would permit the compilation of information by photo interpretation alone. Our literature does not illustrate the kind of photo interpretation keys and aids that were worked out for the military during World War II and reported by Colwell in 1948, nor those for forestry applications as reported by Steigerwaldt in 1950. These kinds of aids and skills are just now being developed for the range resources area by workers at the University of California, Berkeley; at Oregon State University; and at the Rocky Mountain Forest and Range Experiment Station, Ft. Collins, Colo. (Carneggie et al. 1967; Culver and Poulton 1968).

PREMISES, CONCEPTS, AND PRINCIPLES

Few, if any, of the premises, concepts, and principles shown by our research to be important in range resource analysis are new. We claim originality only for the way they are expressed and related to the job of resource analysis (Culver and Poulton 1968).

Cartographic Premises and Principles

Nearly all Federal rangelands have been surveyed at least once since 1911, but many acres of State and private rangeland are still being inventoried for the first time. Whether the purpose of resource analysis is repeat survey or first-time coverage, the maps, legends, and analysis must improve the position of the decisionmaker by (1) improving or strengthening the ecological interpretations of the landscape, or (2) providing a more detailed and accurate picture of the resource and its potentialities to match the growing needs of more intensive management.

In meeting these goals, it is quite common for range resource people to think in terms of the greater practicability of large, highly generalized mapping units. It is not uncommon to encounter the view that detailed resource maps are impractical.

> [PRINCIPLE:] *In the cartographic representation of landscapes, it is better to err by too refined mapping than too broad generalization—information presented should exceed today's needs.*

If the analyst errs by exceeding the informational needs of the manager, or if he presents a picture more intricate than is needed for some applications, it is a simple matter for the user to combine the information on an overlay or variously colored map if he is adequately informed about the resource analysis procedure.

If, on the other hand, the analyst errs in combining detail which the manager needs, the information is lost, and field or interpretive work must be repeated to retrieve the buried information.

Effective use of a more detailed resource analysis does require a higher level of ecological understanding by the user. Often the confusion of a good map and legend merely results from contrast with the gross generalizations and inadequate resource maps the manager has used. The resource analyst who paints a picture of the resource as it is, with sound ecological interpretations, is providing for both today and tomorrow. His efforts should provide more adequate information under the growing concept of "acre management" than do the older surveys. The former are forward-looking resource analyses and the need is merely to gain experience in the use of better tools—a bench saw, when needed, rather than a broad axe.

Resource managers often put pressure on researchers and technical staff men to SIMPLIFY, to provide a set of cookbook rules that always work and are easy to follow. We prefer to operate on the following principle:

You can simplify in a meaningful way,
only that which you truly understand.

Understanding requires that you look at the small pieces. When these are figured out, it is usually quite easy to put them together into larger, "more practical packages." Attempts at simplification ahead of understanding are likely to lead to obscured truth and false conclusions. The manger is left in the dark, and funds may be wasted in analyses based on either oversimplification or untimely attempts at simplification for ill-conceived utilitarian purposes.

It is important for users of the output from ecological resource analyses to understand that if the specific landscapes are inherently complicated, their descriptive legends and mapped representations will appear somewhat complex —BECAUSE THEY ARE! Where landscapes are represented by broad expanses of nearly identical kinds of land, their cartographic representations are simple—often appealing to the practical eye. In contrast, information the manager may need is lost if the former kind of landscape is oversimplified in its legend and cartographic representation.

When the ecology of an area is well understood and when the ground truth-photo image relations are worked out within the framework of this understanding, it is both possible and often desirable to develop mapping legends that simplify or generalize the intricate ecological patterns in the landscape. This permits generalization or the presentation of information with varying levels of cartographic detail. For example, we are working on a resource analysis procedure and mapping legend that may be carried out at three levels of generalization. By working from specific to general in legend development, we are reasonably assured that each succeeding level of generalization will be compatible with the previous level. These concepts should be followed in the preparation and use of mapping legends for ecological resource analysis. Unlike in the past, it will be possible to start with a level of generalization appropriate to anticipated management intensity and then to update the analysis and mapping to meet growing needs for resource information without making a completely new resource analysis. Under this concept, resource analysis and subsequent activities to monitor the effects of management practices can produce a growing reservoir of resource data on a permanent ecological base. Because this kind of information is ecologically rather than land-use oriented, it can indeed serve multiple-use rather than single land-use objectives.

Ecological Concepts

In contrast to many other photo interpretation and resource analysis procedures, here the point of focus is the entire community of plants occupying each ecologically different kind of land. These communities integrate the separate growth factors impinging on the plant community and give a biological expression, through the structure and components of the community, of the net effect of all environmental factors or of the ecological site. Thus, the plant communities provide the best and most obvious basis for delineating ecologically comparable landscapes on aerial photography. The photo interpreter must have a working knowledge of these communities to assign meaningful identifications to each delineation and to produce a map of maximum usefulness.

The following supporting premises, concepts, or principles have been important in our work. These have been selected from a longer list which we have amplified where needed (Culver and Poulton 1968).

(*1*) *Similar plant communities are, in fact, repeated across the landscape and show the resource analyst where the net effect of landform, geology, climate, soil, and history of use is essentially the same.*

(*2*) *Vegetation has become well adapted to disturbance through the evolution of its component species. Therefore, it shows a strong tenacity for its environmental niche, persistence of its characteristics* (*particularly species presence*), *and a strong recovery potential after disturbance. Thus, the key indicators tend*

strongly to remain on the site for the resource analyst to read, once he has discovered what they are.

(*3*) *Successful application of vegetation indicator concepts in determining soil conditions and site quality requires that vegetation-soil relationships be studied at the same point in space and time.*

(*4*) *"Site potential," a concept of great practical importance to managers of vegetation and soil resources, is a function of the inherent ecological characteristics of the land plus resource use and management intensity. Interpretations of site potential, therefore, properly follow acquisition of basic resource information.*

Procedural Concepts and Principles

It is important for users of intensive ecological resource analysis information to understand the differences among (1) management, (2) taxonomic, and (3) mapping units. Lack of such understanding results in confusion both in making and using resource maps for planning and for management decisions.

Users of this information sometimes consider resource maps too intricate and too detailed because they do not understand the difference between management units and mapping units. They sometimes declare that mapping should be done in units that managers believe are of a practical size. Some managers apparently do not realize that the only purpose of the mapping unit is to convey information. No inference is intended that the separately delimited areas should be managed differently and thus that mapping units must be large.

The **management unit** is determined by the resource manager, not the analyst. It defines the physical area to which a particular program of management practices is to be applied. It normally will encompass several mapping units which, together with their legend, describe the characteristics of the management unit and provide the manager with the understanding of the resources that he needs to make wise decisions in matching practices to the land.

The phytosociological classification units mentioned in the previous section need to be differentiated from the various kinds of mapping units that are delineated in order to convey information about the resource. The basic unit of the landscape for classification purposes may be referred to as a **taxonomic unit.** For purposes of this presentation, it is the fundamental ecological unit corresponding to the collective area of similar effective environments. These are denoted by the high degree of similarity in the plant communities that occupy each representative area.

The **mapping unit,** on the other hand, is the area delineated on a map, aerial photography, or mosaic to represent one or more taxonomic units and to convey only information about the landscape. There are two kinds of mapping units. **Simple mapping units** delimit only one taxonomic unit with or without allowable inclusions (fig. 3A). A **complex mapping unit** delimits two or more taxonomic units occurring in such an intricate pattern that they cannot be practicably separated into simple mapping units at the mapping of final compilation scale (fig. 3B). Either kind of mapping unit may contain **inclusions** or fragments of other taxonomic units that are too small to be mapped separately, and these are ignored because they comprise less than a specified percentage (usually 10 to 20 percent) of the delineation as mapped (fig. 3C).

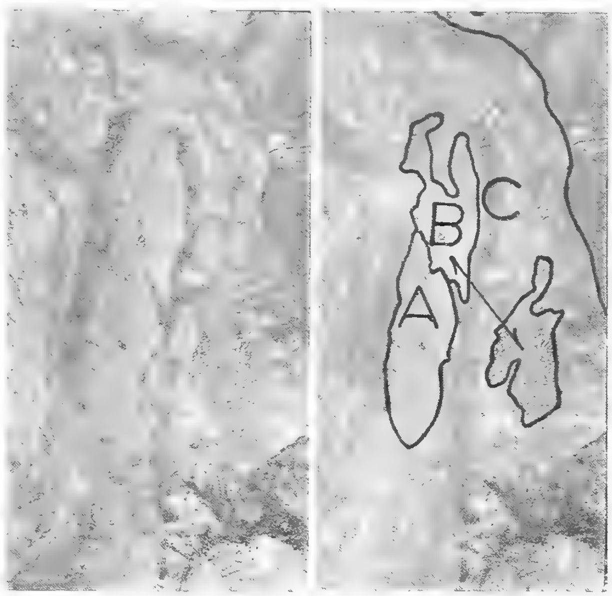

FIGURE 3.—This stereo model illustrates the primary kinds of mapping units.

Our work has led to the development of a set of universally applicable ground rules for intensive resource analysis that set our procedures somewhat apart from common practices in range surveys. These ground rules will result in more easily understood and more readily applied resource analyses:

(*1*) *Strive always to delineate simple mapping units where cartographically feasible.*

(*2*) *Strive to hold complex mapping units to two components* (*taxonomic units*) *per delineation. Three components are allowable. Four can usually be avoided by proper consideration of delineation alternatives.*

(*3*) *Treat complex mapping units by sepa-*

rately examining, describing, and symbolizing each component.

(4) *Allow, as a maximum, inclusions that comprise as much as 20 percent of a delineation; however, it is preferable to hold this limit to less than 10 percent of the delineation area.*

(5) *Differentiate fact and existing conditions from interpretations of the examiner in gathering field data and in preparing initial maps.*

PHOTO INTERPRETATION OF RANGE RESOURCE FEATURES

In doing really serious and effective aerial photo interpretation of rangeland features, people will tend to do a better job if they (1) have keen powers of observation and good stereo perception; (2) have had wide field experience, making astute observations of ecological phenomena; (3) have a logical mind, enabling them to reason clearly and to fit together bits of evidence to form plausible conclusions; and (4) have a vivid imagination tempered by sound judgment. However, range resource people who lack some of these capabilities will be able to glean valuable information from good-quality aerial photographs. Some will do better than others, and a few individuals may only be able to use the photos as field maps. Even if you have been "interpreting" aerial photos for years, it is likely that you will be pleasantly surprised by the increased amount of information you can acquire from interpretation. It only requires that you carefully study the characteristics of aerial photo images and relate the unique images to the phytosociology and resource conditions of the area in which you work.

Useful Image Characteristics

The most successful and accurate aerial photo interpretation depends upon the care with which these subject-image relationships are worked out. Image characteristics that are most useful in the interpretation of range resource features from conventional black-and-white aerial photography follow: TEXTURE of the images of individual plant communities or other features; SURFACE GEOMETRY of items discernible within each image, i.e., within the image of the plant community; PATTERN formed by adjacent images; SHAPES discernible within images, both two- and three-dimensional; SHADOWS of discernible objects; and finally, TONE SHIFT from image to image.

Image tone shift is listed last because it is the most difficult to evaluate in the interpretation of range resource features. Certain technical and operational problems in photography and photo reproduction make it necessary to consider primarily the tone shift, or relative difference in tone, from subject to subject rather than absolute shades of gray. Tone is a very complex image characteristic. In some instances, tone alone is highly significant; in other cases, it can be extremely misleading unless considered along with additional image characteristics.[2]

Additional Considerations

All serious aerial photo interpretation of rangelands should be done under stereoscopic examination. Mapping should normally be done without magnification or under not more than X2 power. After the delineations are made, taxonomic units can be identified; and the reading of other details from the photography is generally best done under X2 to X4 magnification. Except in special cases, higher power usually reduces the field of view so that interpretability tends to be lost despite image magnification.

Where one is working with photography from widespread areas, an important aid to correct interpretation is first to determine the geographic location of the stereo model. With this information, the interpreter is able to identify images from among logical possibilities and to exclude alternatives inconsistent with the location.

Finally, one of the most important requirements to enhance interpretability of aerial photography is to insist on higher standards of performance on image quality control. This applies both to taking photographs and to reproducing prints. Besides the usual contract specifications, more attention needs to be paid to the proper season for photography. In this area, research is especially needed. For grassland, shrub steppe, savanna, and desert areas, high-contrast film types should normally be specified. If range people really want to become serious about remote sensing as a day-to-day working tool, aerial photography specifications should require the use of high-resolution lenses properly filtered to achieve near state-of-the-art performance. Aerial contractors also need help in identifying the more critical vegetation types on which exposures should be based. Negatives should be very carefully screened for quality in terms of image densities and contrast, and experienced vegetation interpreters should be regularly consulted in the review and acceptance of aerial photography. Even if good negatives are available, specifications on print quality are also in order. These should call for a higher degree of uniformity from

[2] For definitions and additional details, consult the *Manual of Photographic Interpretation.*

print to print, and especially from flightline to flightline than has been common practice. We have found that prints from a normal black-and-white negative are more interpretable when processed on contrast 3 paper if the subjects of interest are shrub steppe, grassland, forest openings, or savanna vegetations.

As a standard practice, we always provide a sample print of satisfactory tone values and contrast with all orders for photographic prints, with instructions to match the quality of the sample. All of these guidelines and ideas need further research and refinement; however, until this can be achieved, these suggestions will help one obtain more consistently interpretable black-and-white photography.

Photo Interpretation Aids

When taxonomic units are determined, descriptive legends written, and image-subject relations worked out, various photo interpretation aids are required for the full use of aerial photography as a working tool in range resource analysis and management. We have experimented with three types of photo interpretation aids. All three types have their place in an operational program. They are the kind of items that people must develop for their own areas because the aids must be individualized to the scale, kind, and quality of photography in use on each project. Once the main image-subject relations have been determined for a project area, one should develop these aids to facilitate as many reliable interpretations as possible, and hold additional ground examination to a minimum consistent with the accuracy requirements and objectives of each project. Two of the kinds of guides we have developed are particularly useful as training aids. The third is a reference set of identified stereograms for use in regular project interpretation.

The first training aid consists of a series of full, three-photo stereo models in which unique images are circled, identified by ground examination, described, and the subject photographed on the ground. This material is then organized in a folder for study and reference by the trainee as he relates the ground record to the photo images and studies their characteristics. The central member of such a stereo set is illustrated in figure 4. These sets are chosen by examination and stratification of a flight index mosaic and by selection of one or two stereo models from within each stratum. Stratification is based on similarities of landform, gross vegetation similarities as judged from the small-scale images, and the general patterns of tone seen on the index mosaic. These training sets can also be used as a reference during interpretation if one selects the models from the project area and works outward from each model in the course of pretyping and operational interpretation.

The second type of training aid consists of some carefully selected stereo models assembled in a 2 by 2 or 2¼ by 2¼ format for pocket stereoscope or eyeball stereo viewing (fig. 5). Each model is selected to represent an important subject, but each also includes associated images. The main image in each stereogram is named and thoroughly described. Its identifying characteristics are indicated, and its interpretation is discussed with respect to the following topics: Normal variations, normally adjacent features for which it may be mistaken, associated and convergent evidence, and estimated reliabiltiy of photo interpretation.

The third type of training aid is a working set of stereograms similar to the one shown in figure 5. Only one subject is identified on each stereogram. The stereograms are organized according to the landform on which each is found and on gross similarities of image. These are regularly consulted during the interpretation process, and unknown images are compared with similar stereograms. We hope to develop a dichotomous key to aid in the use of these stereograms and where possible the discrimination of similar images.

By using these kinds of aids, we have developed a reasonably efficient photo interpretation procedure. This utilizes a magnifying mirror stereoscope and a scanning board that permits movement of the stereo model under the field of view and arranges other materials for ready reference (fig. 6).

A REMOTE SENSING APPROACH TO RANGE RESOURCE ANALYSIS

Part of the flow chart outlining the major steps in our resource analysis project for the Oregon State Land Board is presented in figure 7. The complete flow chart covers four pages and contains much more detail, but the one illustrated is sufficient to indicate the maximum level of dependence on aerial photo interpretation in the acquisition of useful information for the multiple-use management of range resource areas. Note that the procedure is, in effect, a double sampling approach. An initial 10-percent sample of the project area was drawn to use in developing both the ecological legend and the photo interpretation keys and aids. With these available, we conducted the project survey by photo interpretation and implemented it by additional ground checking.

We have developed a symbolic legend system that clearly distinguishes between those areas that have been examined on the ground and those that have only been photo interpreted.

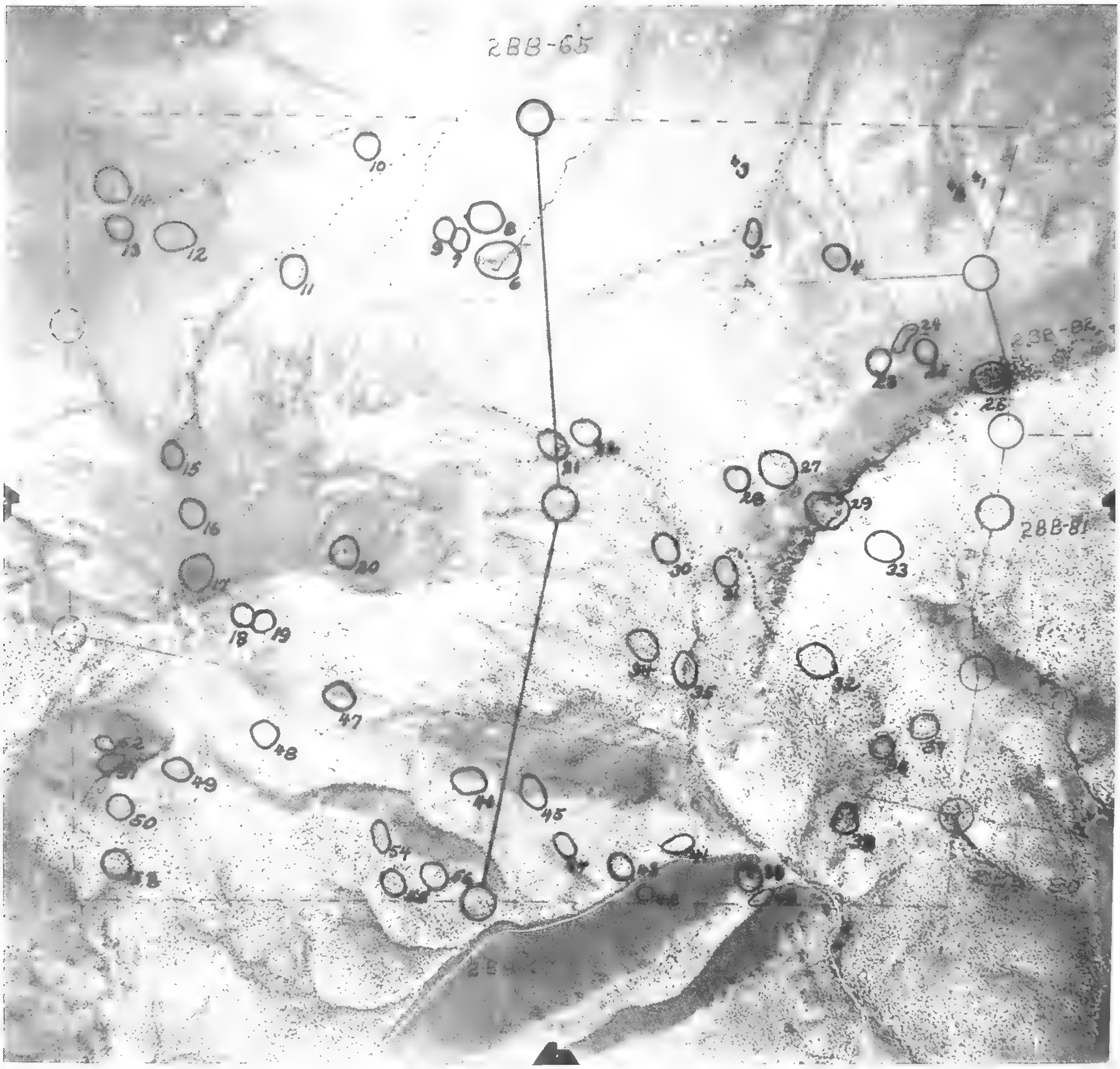

FIGURE 4.—The center member of a stereo model illustrating how unique images are selected for identification and description. Two or more examples of each image are obtained on vegetation and soil conditions represented sary are checked on the ground, and identifying data are circled as potential sample areas. As many as neces- by each image examined. The record is organized into a training aid and reference set from which trainees may learn the image-subject relationships and may develop initial skill as photo interpreters of rangeland subjects.

The legend symbols are expansible, starting with notations of information that can be reliably derived from interpretation. As ground checking is done, symbols are added to convey the kinds of information that can be determined only by ground examinations. Where the interpreters are highly skilled and can make statements about the resource from observed image characteristics and from convergent and associated evidence with reasonable reliability, the symbol system provides for a different notation than where the same information is acquired on the ground. Thus, users of the information are automatically advised of the probable reliability level of data on each parcel.

Resource analyses of this type provide information on landforms and soils characteristics that are relevant to what rangeland produces, to plant communities and vegetation, and to

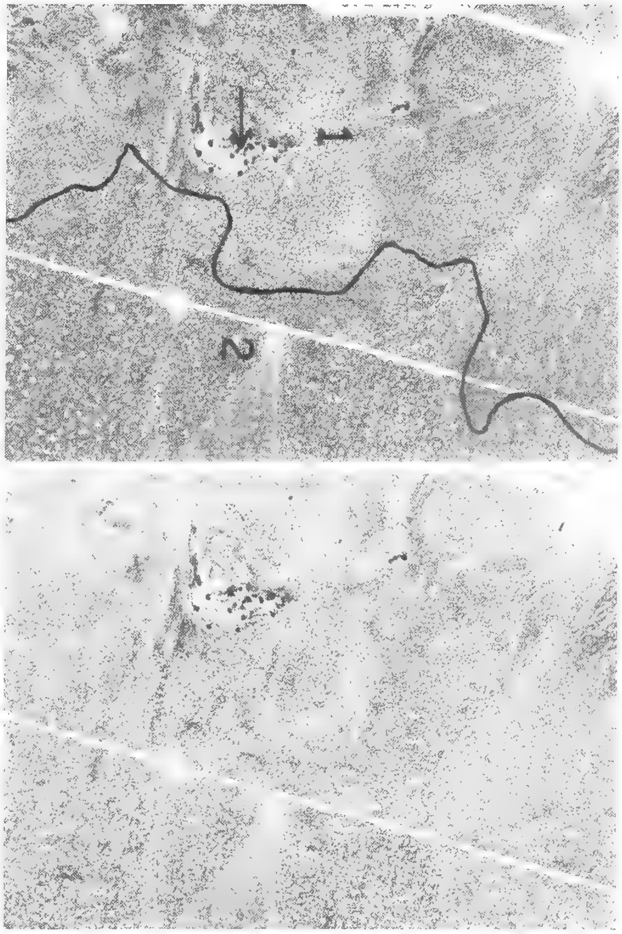

FIGURE 5.—A stereogram developed as a training aid to call detailed image characteristics to the attention of advanced trainees. Each subject indicated in the stereogram is identified and its characteristics are discussed in an accompanying text.

many of the needs of multiple-use management. All this information is being assembled into a descriptive legend and is being in turn related to the symbolic mapping legend for each taxonomic unit. This legend is a permanent working document that presents the identifying vegetational characteristics, the associated landforms and soils characteristics, the interpretations of range condition or plant successional relationships, the ecological potential, and the management implications that are unique to each legend unit. Thus, the descriptive legend will become essentially an operational site guide and technical information source, with daily reference value to the users of the survey. The legend is also a document to which new information about each unit can be added as experience accumulates and as subsequent studies monitor the response of the resource to management.

Because this procedure is fundamentally

FIGURE 6.—A reasonably efficient photo interpretation setup in operation. Binders contain the mapping legend, and the labeled and indexed stereograms are used as references in identifying difficult delineations. The scanning board on which the photos rest permits the stereo model to be moved about under the field of view without disturbing their orientation.

ecological and not utilitarian or focused on a single land use, it is truly a multiple use resource analysis. It presents the inherent ecological characteristics of the landscapes examined, not what the examiner thinks about the resource or is able to infer from his present level of knowledge and experience. We hold that these kinds of interpretations are more properly made after the resource maps are prepared and legend units assigned. By a critical analysis of the facts recorded in an ecological survey, either the examiner or a subsequent user can draw inferences as to ecological climax and current successional status of each delineation. If these decisions are reached separately from the basic mapping job, the conclusions can be graphically portrayed with a system of overlays or variously colored maps. Done this way, the decisions or interpretations of ecological phenomena can be updated and revised as knowledge and understanding grows without destroying the validity of the initial ecological survey. In cases of inadequate understanding of the ecosystems, erroneous judgments as to climax, etc., are not obscured as "fact" in the graphic or legend presentation of the initial resource information. In a similar manner, the data can be examined and interpreted for relevance to any land use or management problem and presented in tabular summaries and/or by a system of overlays or colored maps. Thus, there is really no reason why these kinds of ecological resource analyses will not provide a useful working base for range management, timber management, wa-

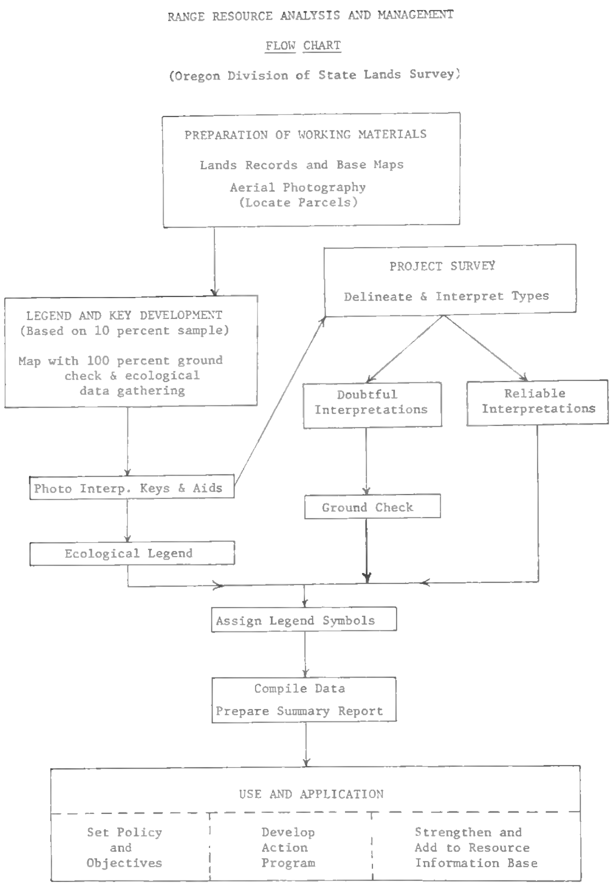

FIGURE 7.—An abbreviated flow chart showing the major steps in a resource analysis program that makes maximum use of aerial photography as a working tool.

tershed management, wildlife management, and recreation development and management of all nonarable land resources. It is the only approach that will put multiple use management on an automatically coordinated common base—an accurate picture of the inherent ecological characteristics of the land from which all these uses are derived. Such resource analyses cannot be prepared without strong reliance on remote sensing and aerial photo interpretation as a means of preparing the maps and as a valuable aid in the identification of similar kinds of land.

In summary, the following four important values are derivable from an ecological resource analysis:

(1) It provides a common base for the accumulation of more resource information related to individual or groups of uses and to results from the application of particular management practices.

(2) It provides the needed stratification base for obtaining data to index or measure the response of the resource to man's manipulative activity. All too frequently past attempts to document vegetation changes have led to the decision "no significant response" when the problem was merely excessive, unidentified variability in the data. The solution to this problem is proper stratification of samples in the acquisition and summarization of data.

(3) It provides an excellent way to extend research results and management practices to ecologically equivalent sites and thus to remove most of the guesswork in the application of information to new areas.

(4) It provides an answer to the question "What is range and forest site?" This resource analysis approach provides a natural basis for determining site potentials for any use or product of the land.

WHERE DO WE GO FROM HERE—

Despite the successes and problems associated with the interpretation of vegetation resources from conventional panchromatic aerial photography, this system of remote sensing is greatly underdeveloped in relation to its potential contribution. This has resulted from problems of quality control and from past conservative attitudes regarding the expenditure of funds for photography that is especially suited to the needs of the range resources analyst.

Conventional aerial photography can tell us far more about vegetation resources than the average technician realizes. Range people have a lot of catching up to do. Let us:

(1) Write and insist on appropriate specifications for useful aerial photography.

(2) Learn to interpret and use in our day-to-day work high-resolution photography of an appropriate scale and season of photography to best meet our needs.

(3) Begin concerted research and management to unravel the community ecology and vegetation-soil relationships to provide the basis for ground examinations that are essential in accurate photo interpretation, and

(4) Become skilled photo interpreters of conventional photography so that we will know both how and when to use the more sophisticated systems that are now lying on our doorsteps ready or almost ready to be picked up and applied in doing a better job of range resource development, improvement, and management in a sound multiple-use setting.

As we move ahead in vegetation resource use development and management in the United States, the combination of resource ecology and remote sensing will place a recording of the resource of unimagined quality at the fingertips of the decisionmaker. Through the combination of these two sciences, resource ecology and remote sensing, we will be able to relegate

more and more of the managers' need for ground evaluation to the era of the "horse and buggy." We in range resource management must capitalize on remote sensing as a day-to-day working tool by developing its full capability.

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70-MM. Aerial Photography—A Remote Sensing Tool for Wild Land Research and Management[1]

JACK N. REPPERT and RICHARD S. DRISCOLL[2]

New remote sensing techniques will be widely used in wild land research and management in the years ahead. A review of our initial efforts with one facet of remote sensing—large-scale 70-mm. color aerial photography—will stimulate appreciation of its vast potential. This potential can be categorized into possibly valuable applications with unique advantages. This system can ultimately be related to more powerful sensor systems, whose efficient use awaits only research and development.

EMERGENCE OF 70-MM. AERIAL PHOTOGRAPHY

While applications of many facets of remote sensing—radar, thermal sensors, etc.—are relatively new to range and related fields, photography is not. In past years, small-scale (1:15,000 to 1:20,000 and smaller) aerial photography has been used, mostly to delineate only very broad vegetation types and physical features. And even that part of the three-step procedure for determining range condition trend that requires oblique ground photography every 5 years depends partly on remote sensing.

Few range and wildlife researchers have appreciated and fully used the potential within conventional aerial photography. We left it to the foresters with the thought "it's difficult enough to detect, identify, and measure a pine tree, not to mention a bitterbrush or Idaho fescue plant."

The breakthrough that now permits detection of small grassland and shrubland features centers around recent technological advances in camera systems and films that permit large-scale, overlapping aerial photographs of high resolution to be obtained. In 1953, Losee called for the use of large-scale photographs to obtain more efficient timber estimates. Seventy-mm. camera systems with rapid film transport and fast shutters (1/1,000 second or faster) were suggested as the best solution to the image motion problem associated with large-scale photographs (Heller et al. 1964).[3] Aldrich (1966) lists several other advantages of 70-mm. camera systems; these include low cost, light weight, interchangeable lens, narrow angles of view, and film easy to process and use in the roll.

High-speed color film, adaptable to the 70-mm. camera system and exposed at large scales, has more potential for species differentiation than ordinary black and white film because there are about 20,000 color combinations distinguishable to the human eye, versus 200 shades of gray on black and white film. More differentiation can be obtained by using color infrared film, which is sensitive to green, red, and near infrared wave lengths of light (blue light is omitted by using a Wratten 12 filter). Resulting photographs exhibit a false color effect. For example, reddish brown soil appears green on the film, and healthy, vigorous, green vegetation appears as some shade of pink or red.

Large-scale photography can be used for (1) tree species identification (Sayn-Wittgenstein 1960, Heller et al. 1964), (2) tree volume estimates (Kippen and Sayn-Wittgenstein 1964, Lyon 1967, and Weber 1965), and (3) forest health determination (Aldrich 1966).

Because of this successful use of large-scale photography in forestry, it is only natural that such a system might prove to be a useful sampling tool for shrublands and grasslands (Carneggie and Reppert 1969).

NEW STUDIES STARTED

In 1967, three feasibility studies were started. The objective was to find the usefulness of two types of aerial film (Anscochrome D–200 and Ektachrome Infrared Aero) taken at various times during the growing season at large scales (1:650 to 1:4,600) for detection, identification, and measurement of herbaceous and shrubby species and other range features. If the system showed promise for these purposes, a procedure could be developed to use this photography system in range inventory procedures.

One study was located at Harvey Valley,

[1] Research reported herein was conducted in cooperation with David M. Carneggie, School of Forestry, University of California, Berkeley, Calif., and R. C. Heller and other personnel of the Forestry Remote Sensing Project, USDA, Forest Service, Pacific Southwest Forest & Range Experiment Station, Berkeley, Calif.

[2] Principal Range Scientist and Range Scientist, respectively, Rocky Mt. Forest and Range Exp. Sta., USDA Forest Serv.; central headquarters is maintained at Fort Collins, Colo., in cooperation with Colo. State Univ.

Calif., on grass and shrub sites within the ponderosa pine bunchgrass area, Lassen National Forest, Calif. (Carneggie and Reppert 1969). A second study was started at Black Mesa on sites within the high-elevation Thurber fescue grassland, Gunnison National Forest, Colo. A third was on shrub sites used primarily as deer winter range in Middle Park, Colo.

In 1968, two more studies were started: one in a pinyon juniper area near McCoy, Colo., and another on sites within the ponderosa pine bunchgrass area at the Manitou Experimental Forest, Colo.

Preflight ground procedures consisted of marking certain plant species and other ground features with arrows (surveyor stakes laid horizontally on the ground) for quick comparative reference on aerial photographs (fig. 1). Rectangular plots were laid out, and the vegetation therein was mapped or photographed from the ground for future comparison with aerial photographs. Line-chart intercept of vegetation, and other ground features along transects within these plots, were measured for comparison with the scan-line output of image color densities produced by a microdensitometer. This instrument, which measures light transmission through photographic transparencies, is affected by the image density of small areas; it is described in more detail by Doverspike et al. (1965). The ground targets were photographed from a stepladder at or near the time of flight, and extensive notes were taken about plant phenology, plant and soil colors, and other factors (fig. 2).

The aerial photographs were taken from an Aero Commander 500B by personnel of the

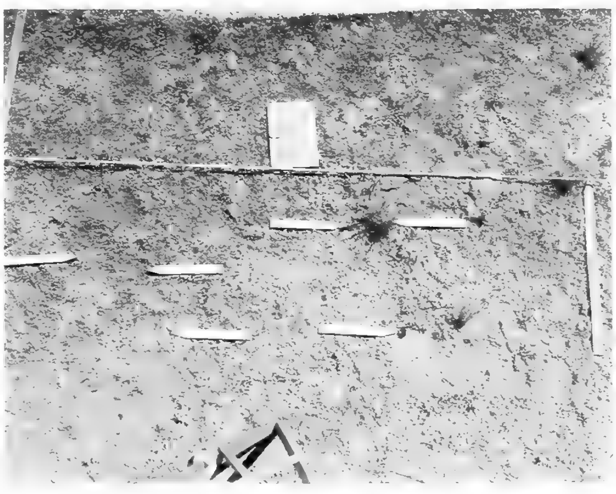

FIGURE 1.—Photo from a stepladder, showing arrows pointing to four species, bare soil, and a rodent burrow entrance. Long lath on right points to zero end of a 20-foot permanent line transect; 10 feet of this transect is shown in the photograph.

FIGURE 2.—Near-vertical ground photographs of marked targets are taken on or near the day of the photo mission, and make up a vital part of the ground truth. Note low-flying photo plane.

Forestry Remote Sensing Project, Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture, Berkeley, Calif. Twin-mounted KB 8A Maurer cameras, equipped with 150-mm. Schneider Xenotar lenses, were used with 70-mm. Anscochrome D–200 filtered with a 1-A Skylight filter, and with Ektachrome Aero Infrared with a Wratten 12 filter. The cameras were impulsed simultaneously with an Abrams CP–3 intervolometer to provide identical photo coverage on the two film types. Shutter speeds were set at 1/2,000th second, with the airplane flying 100 miles per hour, to reduce image motion and to obtain 60-percent overlap for stereoscopic coverage. The photo missions were flown rather close to the ground, some as low as 300 feet, to obtain the large scales desired.

EARLY RESULTS

Several results have been obtained from this first work. Obtaining large-scale color aerial photographs was not an end in itself. In fact, if aerial photographs are taken without regard to season, they may be nearly unusable for desired objectives (see color plate II D and E in accompanying paper by D. M. Carneggie). However, if the necessary time is first expended to find out why things are happening to features shown on the photographs, one can then hope to prescribe situations when color or color infrared aerial photography will be useful.

The best time or season for photography depends upon what range feature is of interest and its stage of development, if it is a plant. For example, at Harvey Valley, Calif., in late July, both color and color infrared film were good for identifying *Eriogonum* spp., which at

that date had many showy yellow flowers. However, infrared was much better for separating *Purshia tridentata* from *Artemisia tridentata* (see color plate II B in accompanying paper by D. M. Carneggie). On the other hand, *Carex exerta,* a low-growing sedge, was only faintly visible in outline on color infrared in July when it was mature and dry; however, it stood out in a bright pink outline on June 10, when it was in a green vegetative stage. The two previously mentioned shrubs—both in early leaf stages—were not so easily distinguished on June 10. The identification relationship between the two shrubs was similar at the Middle Park, Colo., test site.

At the Black Mesa, Colo., test site, photographs taken in July, when all herbaceous vegetation was growing vigorously, provided minimum differentiation among species with either kind of film. However, by late August, when some species were completing their summer growth, species were more readily differentiatable. For example, *Geranium fremontii,* which had developed seed and leaves turning red, appeared gold in the color infrared photographs. No other image with this color characteristic was detected. *Helenium hoopesii* appeared as a pink rosette, brighter in the center than around the edges, on the color infrared. These and other species were not as easily identified in the color photographs (see color plate II C in accompanying paper by D. M. Carneggie).

While it will take several conclusive photo interpretation tests to fully determine how much more useful one film type is over the other, we do have some indication that color infrared has distinct advantages in differentiating species. On three dates, for instance, *Cirsium* spp. consistently showed as unique brilliant red spots on color infrared. For the three dates, *Purshia tridentata* and *Artemisia tridentata* both appeared a very similar shade of green on color film, but on color infrared photos *Purshia tridentata* tended to be a brighter red than *Artemisia tridentata.* A deer carcass, which was placed along the flight line at the Kremmling, Colo., site, tended to show a brighter whitish tone on color infrared photographs taken in August. Thus, it contrasted more with nearby vegetation than with the image characteristic on color film, thereby indicating the feasibility of this film type in assessing winter deer losses.

This initial work with large-scale aerial photography has shown that many features—some surprisingly small—can be detected. A complete list of these detectable features would include the following:

1. Individual shrub, grass, and forb plants.
2. Flowers on forbs such as *Eriogonum.*
3. Larger seed heads on some grasses such as *Bromus inermis.*
4. Colonies of tiny annuals such as Gayophytum spp.
5. Cattle tracks and droppings.
6. Soil surface erosion and surface moisture.
7. Rocks as small as 1 or 2 inches in diameter.
8. Dead deer and shed antlers.
9. Rodent holes and casts.
10. Anthills.

POTENTIAL USES

Because so many features can be seen on large-scale aerial photography, as compared to small-scale photography, prospects are good for developing techniques to:

1. Identify many plant species and soil surface features.

2. Better classify grass and shrub communities into specific habitat types or sites.

3. Measure herbaceous and shrub vegetation parameters such as cover, density, height, spatial distribution, and utilization.

4. Monitor changes in vegetation and in soil surface conditions in relation to time.

5. Monitor natural causal agents of vegetation changes such as rodent, insect, and plant disease outbreaks; and livestock and big-game concentrations, etc.

6. Increase the accuracy of interpretations made from small-scale surveillance systems, such as earth orbital satellite photography, or conventional small-scale aerial photography, within a multiple sampling procedure where interpretations from large-scale photography and ground truth (fig. 2) can be extrapolated to small-scale photography (see color plate I in accompanying paper by D. M. Carneggie). Factors such as precipitation, wildfire, and plant die-off, which often occur uncontrolled over extensive areas, could be monitored by such a system.

7. Relate wildlife dynamics to habitat conditions. Also, by tying in early nighttime thermal sensing of campfires, hunter density and distribution might be related to big-game distributions.

8. Obtain early detection of situations which may have serious management implications, such as influx of noxious plants, unbalanced distribution of livestock, rodent concentrations, and environmental deterioration caused by recreational malpractice such as off-road vehicular travel and littering near hunter camps.

ADVANTAGES OF A PROVEN 70-MM. SYSTEM

An effective technique based on large-scale 70-mm. aerial photography would have many

advantages, most of which would apply to other remote sensing systems:

1. Pictorial backup for ground treatments and measurements. This is the obvious and currently the most common use of photography.

2. A photographic base upon which to make measurements similar to on-ground measurements. For example, line intercept measurements or shrub distribution maps can be made from aerial photographs.

3. Provide a photographic base for new measurements unique to the photograph. An example is the measurement of optical density of specific imaged objects to relate photo image characteristics to species identification or the estimation of some vegetation parameters such as foliar cover, by means of automatic data processing.

4. Provide a permanent photographic record for later examination to evaluate the reasons for unsuspected change or reaction of vegetation to some factor(s). For example, a small colony of annuals, even though unnoticed now, is preserved on film for future viewing should it become widespread and obvious in later years.

5. Eliminate measurement variation due to personnel changes or changing measurement standards by allowing today's photo interpreter to return to yesterday's scene and to simultaneously remeasure both situations by an identical procedure.

6. Shorten the season of field data collection and partially solve the changing phenology problem as it affects measurement of vegetation parameters.

CONCLUSIONS

Our current efforts have been directed toward (1) developing identification techniques and tests for plant species and other wild land features, (2) determining optimum film types and dates for taking photos, and (3) perfecting herbaceous shrub photogrammetry techniques. Included were preliminary efforts to relate microdensitometer measurements to on-ground line-intercept values.

Many problems have been encountered. More intensive ground truth was needed, and will be incorporated into future studies. We found it very difficult to describe color on the photographs, even using Munsell color chips. Thus, the description of photo images based on non-color characteristics (texture, height, shape, shadow, etc.) may be of equal or greater value in identification than color descriptors. However, the use of color descriptors still offers greater potential for identification purposes because the color combinations are greater than the number of gray tones in panchromatic photographs.

There is need for fundamental research into such factors as the physiological causes of different shades of color of plant species as shown on the photographs. There is also a need to develop automated interpretation and analyses by use of a device such as a scanning microdensitometer coupled to a computer system, which would reduce the volume of data in the aerial photographs into usable forms.

Finally, there is need for continued cooperation and open interchange of ideas and developments. This includes contact with scientists and others working with the various sensor systems.

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Animal Census and Other Applications of Remote Sensing in Wildlife Management and Habitat Research in Forested Areas

FOREST W. STEARNS[1]

The use of remote sensing techniques in census activities will be discussed. Possible applications of remote sensing to wildlife and wildlife habitat research will also be suggested. The previous papers have emphasized the general principles of remote sensing techniques, the problems involved in such techniques, the need for ground truth, the unused potential of conventional aerial photography, and the great value of large-scale aerial photography for habitat analysis.

WILDLIFE CENSUS OBJECTIVES

The need for an absolute census of animals or birds is often questionable. Knowledge of population trends is probably as valuable in game management as knowledge of the exact number of individuals. However, in recent years pressures have developed that demand more and more accuracy in estimation of numbers. For one thing, management based on numbers is somewhat more readily sold to the administrator and his friendly critic, the sportsman. Also, as management is intensified, management units reduced in size, kills better regulated, and habitat-environment interactions better understood, the need for better census techniques will increase.

In research on mammals or birds and their habitat, it is often essential to know the number of individuals involved to properly understand the response of both the individual and the population to the changes or conditions being measured.

Cain, in his talk at the 4th Remote Sensing Symposium in 1966, summarized the demand for improved remote techniques for census as follows:

> "There is need for information on population size, occurrence of subpopulations, and distribution in space and time of individual species and associations of different species. There is need for data on recruitment and mortality. Such inventory data are required for fishes, birds, and mammals of importance to man if they are to be granted conservation management, that is, if man is to make nondepletive use of them by avoiding overharvest."

TERRESTRIAL CENSUS METHODS

The techniques now used for animal census will be considered briefly. This is not a complete summary, but it will help put some of the more recent developments into context. Without stretching the definition of remote sensing excessively, it is suggested that virtually all the techniques now in use involve remote sensing. The major exceptions are the trapping or netting methods where individuals are contacted, constrained, banded, tagged, or otherwise marked and released. The second nonremote technique for population census involves the use of age, sex, and kill data. In this method also, the manager has the beast or bird in hand and can determine specific facts about it as well as having positive knowledge that it existed in the population.

What of other census techniques? Track counts are frequently used to determine population trends and habitat use by animals. They represent a form of sensing remote from the animal in time. Track counts are indefinite: one is never sure whether one or many animals were involved in making a specific grouping of tracks. Likewise, when conditions are not right, no tracks are visible.

Like track counts, pellet group counts are remote in time from the animal and usually cannot be referred to a specific animal or time. Populations on large areas can be sampled effectively with pellet group counts. The technique has been highly refined, both in the Midwest and the Far West. It is primarily suitable for large herbivores that deposit a conspicuous and persistent pellet group, particularly when feeding on woody plants. At first, the pellet group count was not considered suitable for summer estimations of populations. However, McCaffery, Creed, and Thompson (1967) of the Wisconsin Department of Natural Resources demonstrated that pellet counting is an effective census for research purposes during the spring, summer, and autumn. Deterioration of pellet groups in the summer is much more rapid, so frequent counts must be made.

By combining a refined pellet group count for the white-tailed deer with knowledge of herd dynamics from age, sex, and kill data, Michigan and Wisconsin scientists have been able to obtain reasonably accurate population figures on which intensive management is now based.

Drives, one of the first management and census techniques used, are also a form of remote sensing. A crew of "beaters" moves through an area, causing animals to move so that they may

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be counted by the beaters or by observers stationed along a terminal line. Obviously, this type of census is expensive and unsuitable for large-scale operations, although the Indians used it effectively for herd control. A similar approach that of simple visual observations made along predetermined and well-defined transects by an observer walking these lines, provided valuable census data in the recent study of the white-tailed deer in Texas (Teer, Thomas, and Walker 1965).

Spotlighting or night-shining, in which the presence of an animal is often indicated merely by the reflection of the projected light from the eyes, is another form of remote sensing. In open areas in the forest, this form of census is useful, although numbers are usually underestimated.

The woodcock peenting census is a form of remote sensing in which the ear is the sensor as often as the eye. A similar technique is the widely used ruffed grouse census method, the drumming count. Problems involved in these techniques are well known and have been discussed in detail elsewhere.

Any form of visual or audio observation should be classed as remote sensing, whether it be searching for eagles from the ground or using a dog and his sensitive nose to flush and thus census grouse or pheasant. Today then, most of our techniques for determining population size and distribution are not based on contact, but on indirect or remote approaches.

AERIAL CENSUS METHODS

The aerial surveys of big-game animals more closely approach the modern concept of remote sensing. For some years Minnesota and Ontario as well as other Canadian provinces and Alaska have regularly censused moose by intensive aerial surveillance over designated sample areas. They have found it more effective to use trained observers than to take and then interpret aerial photographs. The aerial observer can zero in on a questionable spot, and the pilot will circle lower until he frightens the animal out of the brush.

Aerial observation for census purposes has been used extensively in Africa; the work of Darling (1960) is a good example.

The aerial photography (both motion and still pictures) of wolves on Isle Royale, taken under the direction of Allen and Mech (Mech 1966) provided census data on the wolfpack. The pictures are supported by visual counts in which individuals are identified. Aerial observation is presently being used for many other census needs. For example, Wisconsin conducts a visual aerial survey of breeding waterfowl on 60 transects that are each 50 miles long. There is added benefit in using a human as the sensor; i.e., the observer can often identify the species of bird seen.

The usefulness of aerial photography in enumerating waterfowl in large concentrations has been demonstrated, particularly for the Pacific Coast flyway (Chattin 1952). With low-level photography, the interpreter can readily count birds and, when necessary, subsample the pictures. Recently Kadlec and Drury (1968) reported on a method to determine trends in gull populations by combining visual estimates of numbers with photography of both the island nest areas and the flocks of birds utilizing the islands. They state, "Test predictions of the numbers of nests from counts of gulls on photographs gave acceptable results even for most individual colonies," and "Neither visual estimates nor photography will reliably detect annual change of less than about 25 percent." (in the breeding gull population)

Wisconsin and other States use aerial sensing for checking on a variety of water activity. Boating and fishing surveys made from the air provide knowledge of people-pressure on lakes of different sizes and at different times of day. Water skiing is also censused by aerial observation.

Thus, aerial sensing techniques are not new or unusual in wildlife population census, and they can be expected to increase. The question is how effective and economical will we find the highly sophisticated sensing methods now being developed for other aspects of the evaluation of natural resources.

As Poulton indicates in his conference paper, few range and wildlife researchers have fully appreciated or fully used the potential of conventional aerial photography. There is much useful information on these photos for habitat evaluation, and perhaps also opportunities for population evaluation. Aerial photography has little application to pellet group counting; on the other hand, Reppert and Driscoll (1968) suggest in their conference paper that it might be very useful for species that produce casts or burrows. Photography is effective only when the object to be photographed can be detected in the picture. So much of the ground surface is screened by vegetation in the Lake States and Northeast that not only is aerial photography of limited value for counting animals, but other forms of remote sensing, such as radar and infrared scanning, may also be severely limited. Seasonal changes in cover with spring, fall, or winter aspects sometimes provide good opportunities. However, animal habits in relation to cover, wide distribution of conifers, and other factors tend to amplify the influence of the tree canopy.

Nonetheless, aerial photography is useful in

census work, particularly for concentrations of wildlife such as elk herds, for flocks of migrating ducks and geese, and for people (our greatest problem species). Photography should be more widely used.

PHOTOGRAPHIC RANGE INVENTORY

In a paper prepared for the 1968 Remote Sensing Symposium, Huddleston and Roberts (1968) described the use of photography for livestock inventory. In the past, livestock inventories have been made by ground counts of each of a number of sample areas picked from aerial photographs. To reduce the number of ground surveys, photographic techniques were recently developed and tested in the Sacramento Valley of California. Complete stereoscopic photo coverage (black and white) of the sample areas was obtained at a scale of 1:5000. At the same time, a subsample was photographed in color at a scale of 1:2140, covering about 40 percent of the sample area. Photography was limited to morning hours in the spring; the green grass provided excellent interpretation background. Concurrent with the photography, ground crews sampled the same fields to obtain data on both crops and livestock.

Prior exploratory work had shown that green grass gave better contrast than brown grass for counting sheep, and gave reasonable contrast for identifying cattle. The time of day was also shown to be important. Animals tend to be in the open during the early morning and early evening hours. Although these are not optimum periods for photography due to sun angle and poor lighting, it is essential that the animals be where they can be seen. Shadows may hide an animal, but they are also helpful in identification. Likewise, increased accuracy in enumeration with stereoscopic coverage was well worth the added expense over nonstereo-coverage.

It had further been determined that a scale no smaller than 1:5000 was necessary if livestock inventories were to be highly accurate. A Wratten 25A filter was used to improve haze penetration and to increase contrast.

Huddleston and Roberts divided their sample into a cultivated stratum and a range stratum. In the cultivated stratum, reliability of numbers was somewhat better except where clutter from manmade shields (barns, sheds, etc.) was present. Tall obstructions effectively shielded animals. An inventory of the range stratum involves other difficulties. There is more background clutter and isolated animals may be missed; the ground data are also less accurate. The authors state that prior to a suitable survey, some preliminary sampling is necessary to properly stratify habitat and to obtain a check of ground truth reliability. For wild animals this would be difficult to do; however, the next study to be discussed represents a situation in which it was accomplished.

Huddleston and Roberts concluded that more efficient techniques and equipment for rapid interpretation are needed before operational surveys are undertaken. However, these advantages make photographic survey worthwhile: (1) Access to remote areas is easier; (2) large areas can be covered quickly; (3) certain biases of ground surveys can be eliminated; and (4) the count has greater objectivity. They state:

> "It seems likely that the use of aerial photography to supplement conventional enumeration methods can lead to an improvement in the quality of livestock inventory statistics . . .," and "The first effort to introduce remote sensing into an existing data collection system might be done most judiciously by incorporating it into the quality control or re-enumeration phase of the survey."

INFRARED SCANNING AND RADAR

Croon, McCullough, Olson, and Queal (1968) tested the use of infrared scanning techniques for big-game census on the University of Michigan George Reserve deer herd. The George Reserve, a 2-square-mile area near Ann Arbor, Mich. contains a population of white-tailed deer estimated by various methods at about 100 animals. Vegetation on the Reserve includes open grassland, hardwoods, and a limited area of pine. To extend the test, three deer were placed in small pens under different cover conditions—open grassland, hardwood canopy, and pine canopy. Radiometer (Stoll-Hardy screened for infrared) readings made at the time of flight showed the temperature of the penned deer and their background differed approximately 7° C. The authors report that the deer in the grassland and oak woodland were easily detected on the imagery, but the deer penned under the conifer canopy would have been missed if its location had not been definitely known.

The equipment used was an imaging infrared scanner, a line-scanning device related to the TV camera. It includes three components: A mechanical scanner, a detector, and a signal display system. The heart of the instrument is the detector; in this case, it is sensitive to longwave infrared energy. The authors point out that the surface characteristics of an object control its emissivity of radiation at any given temperature, and they define the apparent temperature as the product of emissivity and the actual temperature (in degrees abso-

lute). They state that the 8- to 14-micron band seems to be the optimum wavelength region for infrared detection of warm-blooded animals. They say, "To be detected as different from its background, an animal must emit (or mask) enough energy to produce an instantaneous response, averaged over the entire field-of-view, which is greater (or smaller) than the response produced by the background alone." In their study the field-of-view was approximately 3 feet in diamter; thus, few game animals would completely fill it. Ground measurements were used to test whether or not rodents or birds would be confused with larger animals. These measurements indicated that at the altitude flown, it would be difficult to detect a fox and that it would be impossible to detect smaller animals.

The test on the George Reserve was made at noon on January 4, 1967, when the Reserve had a snow cover of 6 to 8 inches and the air temperature was approximately 25° F. Daytime sensing with a snow cover and overcast sky (warm air) appeared most appropriate. Imagery was obtained from an altitude of 1,000 feet, and seven flight lines were used for complete coverage. Imagery was interpreted by the infrared physics laboratory of the University of Michigan, and the hotspots were identified as deer by the interpreters. These were subsequently field checked to be certain that a permanently hot target did not exist at that point. Ninety-eight animals were detected.

In this test, the 7° C. differential in infrared emission between the deer and background was well within the detection range. The temperature differential was nearly ideal, but detection would be possible with a lower differential. Different vegetation types gave approximately the same apparent temperature. The evergreen canopy on the Reserve is limited, and no deer were in the area during the flight. The noon timing of the flight probably reduced any possibility of fox or racoon being detected since they would tend to be in their dens. The authors concluded that infrared scanning . . . . "may give good census figures on big game populations in relatively open canopies; for example, counting of deer in hardwood stands in winter, and in low brush and censusing open range animals such as caribou, antelope, bison, etc. Since the technique involves heat rather than visible light, scanning could be done at night when animal activity is frequently highest."

Results suggest that under a conifer canopy and probably under a hardwood canopy, many animals would escape detection. At present the method is extremely expensive and is probably feasible only when a scanner could be used in conjunction with other applications, such as detecting forest insect damage or water pollution. More details are available in a recent paper (McCullough, Olson, and Queal 1968).

The two studies discussed above suggest that for some time in the future, sophisticated remote sensing techniques will not have wide use in game census procedures. In special situations, they may be valuable—for instance, in large-scale photography for censusing concentrations of animals or waterfowl. And certainly photography, with or without infrared scanning, is valuable for sampling concentrations of big-game animals in open range like that on the African Veldt.

It appears doubtful that radar scanning will have much application in mammal studies in the near future. However, radar has an interesting potential because it can penetrate rain, clouds, tree canopies, and even soil; if suitable wavelengths can be used, the returns from trees, soil, and animals can be separated and the animals thus counted. Despite its present limitations for mammals, radar scanning has been shown to have utility in following bird movements, especially where the bird is silhouetted against the sky. Work in this area has been in progress since before 1958 (Tedd and Lack 1958). A major problem has been accurately estimating numbers of birds from the radar returns. By calculating size of the echoing areas of individual birds, Eastwood, Isted, and Rider (1962) were able to estimate the number of birds in a roost from the radar returns on departure flights from the roost. The use of radar in ornithology has been summarized by Eastwood (1957).

In a recent paper, Dyer (1967) describes a scheme for analyzing scan by motion picture filming of bird movement on the radar screen. He used the technique to determine relative densities of redwing blackbird flocks moving in a concentration area in North Dakota. Reflections from buildings and shelterbelt plantings caused problems in the study of the local low-flying flocks.

REMOTE SENSING IN WILDLIFE RESEARCH

What other opportunities are there for aerial remote sensing in wildlife work? The author's initial interest concerned the potential of infrared scanning for investigating the use of forest openings by white-tailed deer. We were hopeful that by scanning at night we might determine animal use for many openings, as well as the size of openings favored by the animals. This is still a possibility, although the opportunity for such study is now remote. Another application that might be investigated

is the use of infrared scanning to locate and count active beaver lodges during the winter. The heat emitted from the closed lodge of a colony of beaver might provide an interpretable hot spot on the scanning imagery. However, the early autumn aerial observations now used are relatively inexpensive and accurate.

Remote sensing techniques should not be limited to aerial applications. There are many opportunities, especially in research, to use various remote techniques on the ground. These techniques may consist of infrared scanning or infrared propagation methods to detect the presence of animals, or of triggered flash photography and the use of odors and sounds for population census in small areas. Automated systems for some of these techniques will be especially useful.

Space and subject limitations preclude discussion of other forms of remote sensing, such as the determination of body temperatures by scanners or of the remote sensing of temperature and physiological parameters using telemetry. The use of telemetry to follow the movement of wildlife species is well established, but defies review in this short paper.

CONCLUSIONS

It is hoped that it has been made clear that the emerging sophisticated sensing techniques do not represent a panacea for all the problems of wildlife census. However, large-scale and color photography, infrared scanning, radar, and other approaches may be extremely useful in some situations, and their development and refinement should be followed closely by those involved in wildlife census.

It would behoove wildlife researchers to explore the present and potential uses of large-scale 70-mm. photography, especially in habitat work, and to keep abreast of developments in other forms of remote sensing. Progress in infrared scanning and in radar in particular should be closely followed, so that when better hardware becomes available, the researcher will be in a position to use it.

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RANGE AND WILDLIFE HABITAT ECOLOGY—STATUS AND CHALLENGES

Range Ecology in the Western United States

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EARLY ECOLOGICAL RESEARCH

From its beginning in the 19th century, with cursory observations and collections of plant and animal specimens, range ecology in the West has progressed to where it now receives careful study from highly trained specialists using sophisticated techniques and equipment. As general ecological knowledge has been accumulated, as study techniques have been developed, and as related disciplines have contributed, increasing impetus has been given to range ecology investigations. This paper reviews briefly the development of range ecology in the West. It also includes a general resume of present knowledge and of the future needs of research.

Some of the earliest ecological information on rangelands was obtained by surgeons who accompanied military expeditions in the West (Emory 1848). Somewhat later, agricultural specialists made general observations of range conditions, plant identification and distribution, and forage value (Vasey 1889; Smith 1895; Rydberg and Shear 1897; Williams 1897; Nelson 1898; Clements 1920).

Shortly after the turn of the century, range ecology investigations were enhanced by the establishment of several range experimental areas; e.g., Santa Rita Range Reserve near Tucson, Ariz.—1903, Great Basin Experiment Station at Ephraim, Utah—1912, Jornada Grazing Reserve near Las Cruces, N. Mex.—1914, and experimental pastures at Mandan, N. Dak.—1915, and at Ardmore, S. Dak.—1917.

Quantitative measurements of range plant communities were reported from the Santa Rita Range Reserve by Griffiths (1903), Thornber (1910), and Wooton (1916). The Office of Grazing Studies in the U.S. Department of Agriculture began range ecology studies in northwestern Oregon in 1907 (Jardine 1908; Sampson 1908). Subsequently, investigators attached to National Forests in 1911 sought information on the occurrence, reproduction, and economic values of forage plants, and also the establishment of ecological principles for the conduct of proper grazing management.

The concept of "succession" was an important milestone in the development of early ecology. Some examples of American contributions to the concept follow. Cowles (1899) described plant succession on sand dunes of Michigan. Clements (1904) proposed that a vegetational community is an entity, which performs in accordance with certain basic biological principles, as do individual plants. Shelford (1913) pioneered investigations of animal succession, reporting on the relation of tiger beetles to the plant changes described by Cowles. Clements (1916) further promoted the idea of climax. In fact, he regarded succession as the life-history of a climax formation. Sampson (1919) applied the prevailing concept of plant succession to mountain bunchgrass rangelands. He contended that livestock grazing could effect either "progressive" or "retrogressive" succession, depending upon the amount, kind, and time of livestock grazing.

Studies of reactions of individual plants to top removal and grazing led Sampson (1913) to conclude that repeated herbage removal retards growth the following spring and reduces physiological vigor for full reproduction,

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whereas removal of herbage after seed maturity does not interfere with plant growth—the basis for recommending grazing deferment systems. Sampson (1914, 1917) also studied the life history and growth requirements of several important range plants, both under grazing and under protection.

In the Great Plains regions, Briggs and Shantz (1913, 1914) determined the water requirements of some native grasses and forbs. Weaver (1914, 1919) reported on important ecological studies concerning grasslands, particularly with regard to root relations.

The text on plant ecology by Weaver and Clements (1929) stressed developmental taxonomy of plant communities and provided elaborate descriptions of plant formations in North America. In animal ecology, texts by Pearse (1926) from the United States and Elton (1927) from the United Kingdom, probably had the greatest impact upon ecological thinking. Primary interest of both plant and animal ecologists was the distribution of the animal community, its structure and organization, and its temporal development and change.

RANGE ECOLOGY: 1929–45

Range ecology was given impetus by the McSweeney-McNary Forest Research Act of 1928, which extended and intensified the USDA Forest Service research program. Also, during the Great Depression, establishment of such agencies as the Civilian Conservation Corps, Works Projects Administration, and National Recovery Administration brought conservation research and action to national attention. Also, a number of additional experimental ranges were established. Agricultural Experiment Stations at State Colleges expanded their studies in range ecology: Linney et al. (1930) in New Mexico, Hanson et al. (1931) in Colorado, and Brinegar and Keim (1942) in Nebraska (Chapline et al. 1944).

Illustrative of fundamental range ecology studies during this period are those in: Environmental relations—Nelson (1934), Lister and Schumacher (1937), Humphrey (1937), Craddock and Forsling (1938), and McGinnies and Arnold (1939); succession, indicators, and conditions—Campbell (1931), Talbot (1937), Sampson (1939), McGinnies et al. (1941), Pickford and Reid (1942), and Ellison (1949); woody plant invasion—Parker (1939), and Young et al. (1948); and range and wildlife relations—Vorhies and Taylor (1933, 1940), Nichols (1938), and Arnold (1942).

In general, ecological research during this period was exceedingly active, both in quantity and quality of studies. Ecological theory began to mature as a result of development and coordination of biological principles. Moreover, theory was based upon sound empirical evidence rather than upon speculation (Allee et al. 1949).

In range ecology, workers were now aware that: (1) Ecology was a state of mind, i.e., an ability to relate biological facts correctly; (2) life processes operated on a revolving basis and that ecological systems were interdependent; (3) life processes were subject to natural laws, and man could manipulate some but not all of the forces involved; and (4) ecological thinking could not be applied exclusively to either plants or animals; instead, the entire biotic complex had to be considered as the basic operating unit.

POST WORLD WAR II CONTRIBUTIONS

After World War II, grazing studies based upon range ecology were reported for a diversity of range plant communities from experimental ranges previously established. Highlights of these studies are summarized in table 1. Other research centered on life history studies of major range plants, invasion processes of rangelands by woody shrubs and trees, range condition classification, and timber-livestock-wildlife relations. Many of the latter studies were closely related to applied research involving various aspects of management on the western ranges.

Life history studies.—A number of life history studies of range vegetation were reported during the postwar period: Reproduction of southwestern grasses (Canfield 1957); growth habits, habitat requirements, phenology, root systems, soil relations, and diseases of cheatgrass (Klemmedson and Smith 1964); seasonal development and annual yield of individual forage species in relation to climatic factors for the sagebrush-perennial grass association of southern Idaho (Blaisdell 1958); root systems, growth and development, reproduction, genetics physiology, and enemies of bitterbrush (Hall 1964; Nord 1965); growth habits, geographic distribution, poisonous properties, invasion and its causes, and relation to grazing and competition with forage plants of burroweed (Tschirley and Martin 1961); ecological studies of pinyon and juniper (Arnold et al. 1964); and intensive studies of the root systems of range plants (Weaver 1958).

Woody plant ecology.—On the invasion of grazing lands by woody plants, Humphrey (1958) reported that mesquite, creosote bush, cactus, burroweed, and snakeweed were among the principal invaders in the Southwest. He concluded that since the introduction of livestock, reduced plant competition, fire suppression, and rodents have favored woody plants at the expense of perennial grasses. Glendening

and Paulsen (1955) concluded from intensive studies of the factors affecting reproduction and establishment of velvet mesquite that this shrub is well adapted in southern Arizona for further spread into adjacent grassland areas.

Planned burning of sagebrush-grass ranges was found to reduce sagebrush and to be ultimately beneficial to shrubs with strong sprouting habit and to grasses and forbs with rhizomatous growth habits (Blaisdell 1953; Pechanec et al. 1954). However, nonsprouting shrubs, suffrutescent forbs, and some of the finer bunchgrasses were found to be injured severely by fire.

Range condition.—Knowledge of primary and secondary successional trends proved especially important for classifying different vegetation sites in relation to space and time (Costello 1956). Parker (1954) proposed that each range condition class could and should correspond to a stage or group of stages in secondary plant succession. Ellison (1959) observed that trends in secondary succession could be reversed by skillful management where the soil mantle was still intact and where a seed source was available. In a literature search, Ellison (1960) was unable to find substantive evidence that plants were dependent upon animals in the ecosystem. In fact, he concluded that the evidence favored parasitism of plants by animals, even though the evolution of modern grazing animals coincides with the evolution of grasses (Taylor 1949).

Timber-livestock-wildlife relations.—Competition between cattle and deer was recognized on the North Kaibab (Julander 1937) and led to cooperative studies by the USDA Forest Service, the USDI Fish and Wildlife Service, and the Utah Game and Fish Department. Julander (1955) found competition for forage between deer and cattle varied by specific sites. Deer were able to utilize large areas that were inaccessible to cattle because of steepness of slope and unavailability of water and forage. Desirable forage, exposure, and cover largely limited deer distribution in midwinter.

On range used by antelope, Buechner (1950) found that the most important factor affecting the increase and distribution of antelope was intense food competition with domestic sheep. Competition between cattle and antelope was only slight, and antelope appeared to prosper on cattle ranges.

Leopold et al. (1951) and Longhurst et al. (1952) contended that herd regulation was the first step in deer management, and that range improvements were applicable to some deer habitats. Biswell et al. (1952) found that planned fire could be used to improve chaparral habitat for deer. Later, Taber and Dasmann (1958) reported that food quality is the main factor limiting most chaparral deer populations, and that habitat improvement should focus on the introduction of winter forage and the quantitative increase of existing palatable browse.

In the Southwest, Reynolds (1964) found that conservative, selective logging improved deer habitat. Also, deer used pinyon-juniper woodland in proportion to palatable shrub density; by reducing tree overstory to enhance shrub production, habitat conditions for deer could be improved.

Most studies of rodent-range relations during this period showed that pocket gopher control was necessary for improvement of mountain ranges (Moore and Reid 1951; Colorado Cooperative Gopher Project 1960). On California annual grasslands, Howard and Childs (1959) found fewer gophers on grazed pastures at the San Joaquin Experimental Range because of insufficient food and cover.

On mesquite-snakeweed sites of southern New Mexico, rodents and rabbits alone exerted sufficient grazing pressure to preclude vegetation improvement (Norris 1950). Control of these animals was necessary for range improvement but was unjustified economically. For desert grassland ranges of southern Arizona, Reynolds (1958) found that where grazing was so heavy it lowered perennial grass density, the number of Merriam rats increased.

CONCEPTUAL REFINEMENTS

By 1960, basic ecological concepts had become widely adopted in range and wildlife habitat management and research. Dyksterhuis (1958) summarized the state of knowledge relative to range ecology: By 1960, ecologists had become increasingly aware of *energy pathways.* Utilization of energy was known to affect food chains, which, in turn, affected the numbers and kinds of animals associated with rangelands. *Reproduction* mechanisms were recognized as basic to all ecological systems. In addition to their function in transmitting hereditary characteristics, evidence was accumulating that population density, quality of food, and other environmental factors also affected reproduction. *Competition* was credited as being a potent force that gave expression to an ecological community.

There was an awareness that the physical and biotic factors of the environment were in *dynamic equilibrium* in natural communities. It became more fully accepted that *fire* was an environmental influence which supported the evolution and maintenance of some grasslands. *Stratification* as a structural characteristic of a community in both vertical and horizontal dimensions was better understood; i.e., a woody overstory, half shrubs, herbaceous plants, moss, lichens, and microfauna and flora of the

soil were vertically stratified and had their own peculiar environment, which interacted with the larger complex. Horizontally, difference in aspect, insolation, soil, and other physical factors produced different but interacting subcommunities. Appreciation of *ecological balance* or homeostatis in ecological communities was leading to fuller understanding of ecological complexes. Ecologists were also gaining a greater appreciation of the *genetical basis* for many events within biotic populations.

THE ECOSYSTEM CONCEPT

Earlier ecological workers were cognizant of the multiplicity of environmental factors affecting the growth, reproduction, and survival of individual organisms. It became increasingly apparent that not only a multiplicity of factors existed but that their interrelationship was highly complex (Daubenmire 1947). Although attention might be focused on any level, or group within a level, it was recognized that a larger ecosystem was involved. The ecosystem approach visualized habitat, plants, and animals as one interacting unit, with materials and energies passing in and out of various aspects of the entire system (Woodbury 1954). Odum (1953) succinctly defined the ecosystem as:

> "Any entity or natural unit that includes living and nonliving parts interacting to produce a stable system in which the exchange of materials between the living and nonliving parts follow circular paths is an ecological system or ecosystem. The ecosystem is the largest functional unit in ecology. . . ."

Range ecologists recognized the importance of the ecosystem concept in vegetation community processes and related management problems. For example, it was recognized that management which regulates kind and numbers of livestock, predator-control programs, noxious-plant control, reseeding, and fire control modifies the ecosystem (Humphrey 1962). Such an outlook broadened ecological research and enhanced subsequent management (Costello 1957).

Mathematical models and high-speed computers are now being employed to sort out and evaluate the multitudinous factors comprising range ecosystems. As biological and physical components of the ecosystem are measured, simulation models are designed to provide specific answers to highly complex problems. By doing this, many realistic assumptions are handled simutaneously so that alternative outcomes or products are provided. Many hypothetical constraints are tested without long, costly field investigations. Furthermore, simulation analysis often provides insights for additional field investigation.

Limitations to ecosystem analysis of ecological problems must also be recognized. Definition of ecologically natural units poses a real problem (McIntosh 1963). Discrete ecological units, as evolving entities, may even not exist. Until natural units can be demonstrated in terms of genetics and evolution, inherent limitations are posed by complexities of ecosystems.

FUTURE ECOLOGICAL RESEARCH

Numerous areas of research in range ecology should be strengthened to provide pertinent information for forage management of rangelands in the West. Such information seems especially desirable in view of the current attention being given to ecology in relation to man and to improvement of the quality of man's total environment.

Costello (1964) has suggested that range ecology research could be intensified in the areas of: Basic studies of soils, physiology, and ecology; development and improvement of methodology; and the investigation of predicting equations. Knowledge of plant chemistry and physiology in relation to herbage removal is incomplete for understanding the reaction of the plant to the grazing animal. Many birds, mammals, reptiles, amphibians, and invertebrates are found on rangelands, but there are few studies of range wildlife besides those of game and rodents. Studies of micro-organisms, insects, and diseases on rangelands are almost nonexistent. Utilitarian-oriented studies are needed; these should emphasize relations among these organisms, the grazing animals, and the plant and soil.

Public concern is stimulating scientific investigation of the effects of herbicides and pesticides on the range biota. However, range ecologists are devoting only minor effort to this field of research.

Telemetry is another important tool for investigating ecological problems—particularly animal movements on a daily, seasonal, or periodic basis (Hawkins and Montgomery 1969).

Cloud seeding still has realistic possibilities of inducing weather changes to benefit man. Profound changes in natural flora and associated fauna may result, and range ecologists should be prepared to state where and where not weather modification will benefit their interests (Battan and Kassander 1962).

For many years the USDC, ESSA, Weather Bureau has monitored climatic conditions in the United States, but biologists have been lax in monitoring biotic communities over long periods. Studies are needed that monitor the en-

tire complex of soils and vegetation,—with and without livestock and game grazing.

In this connection, baseline areas are needed for checking long-time changes in vegetation where disturbance by man is minimum. Remeasurement of these areas, with reference to climatic conditions, could provide valuable information as to long-time changes in plant communities. Such measurements will be improved with better methods and techniques.

Information is now accumulating as to the effect of chemical stimulants or inhibitors within biotic communities. As an example, analysis of plant selections by certain butterfly groups has shown clearly that plant choice has a chemical basis (Ehrlich and Raven 1967). Knowledge of the factors affecting animal-plant relations in range studies may be quite enlightening as more is learned of the chemical basis for such relations.

Radioecology and radioactive tracers are receiving attention; however, few people trained in range ecology are involved in these avenues of research.

The increasing interest in ecosystems makes imperative studies to measure all effects of grazing (e.g., on native animals, soil, flora, and fauna) within a single biotic community. Systems analysis using high speed computers provides a holistic approach to the analysis of complex ecological problems. The approach provides techniques and theories for analyzing systems of interlocking cause and effect pathways which are common in ecology. Range ecologists should be taking greater advantage of this new discipline (Watt 1966).

To supplement ecosystem analysis, more attention needs to be directed to the efficiency of energy conversion. Energy investigations of ecosystems are being pursued in some biological research which relates reaction rates, organism temperatures, and energy flow at the molecular level (Gates 1963). Energy pathway studies are limited, however, for biotic communities involving rangelands. Studies of ecological processes in terms of energy relations, irrespective of utilitarian aspects, are needed.

Range ecologists have mostly ignored the genetical basis for plant community events. There is evidence that genetical changes within a species population can cause important ecological events, e.g., invasion of a species into a plant community, genetic selection adapting a particular population of organisms to a specific environment, and genetic selection in the evolution of a plant community (MacArthur and Connell 1966). The same deficiencies exist in regard to animals of a biotic community.

TABLE 1.—*Significant range research contributions—post World War II period*

Vegetation type	*Author*	*Conclusions*
California annual grass association.	Bentley and Talbot (1951).	Intermediate degree of grazing maintained adequate litter without apparent soil deterioration or decrease in forage plants.
Desert mixed shrub-grasslands.	Reynolds (1959).	Perennial grass growth is dependent upon summer rains; grazing must be deferred periodically to maintain forage species.
Black grama association.	Paulsen and Ares (1962).	Drought reduced black grama by the same amount irrespective of the degree of grazing, but recovery was more rapid with light use.
Pine-bunchgrass.	Johnson (1953), Hormay and Talbot (1961).	Selective overgrazing by cattle could not be avoided; provision should be made for resting the range.
Mountain bunchgrass.	Beetle et al. (1961).	Litter disappearance was first evidence of range deterioration; continued heavy grazing caused reduction in vigor and loss in cover and production.
Alpine ranges.	Johnson (1962), Smith (1965), and Johnson (1965).	Hairgrass and agoseris were key forage species.
Northern Great Plains.	Hurtt (1951), Reed and Peterson (1961), Holscher and Woolfolk (1953), and Houston and Woodward (1966).	Amount of grazing varied widely because of drought and resultant forage production; heavy grazing reduced litter cover, root volume, organic matter, and noncapillary porespace; plant cover changed with stocking rates on summer range but not winter range.
Central Great Plains.	Klipple and Costello (1960).	Short grass reacted slowly to grazing.
Southern Great Plains.	McIlvain and Lagrone (1953).	Blue grama and forbs increased with heavy rotation grazing.
Northern Desert shrub.	Hutchings (1954).	Desirable shrubs increased under moderate grazing.

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Current Status of Range Ecology in the Southeast

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Ecology is a special challenge to range and wildlife scientists in the Southeast. We know, from limited probing, that ample opportunities are available to modify communities economically, and that rapid, often radical plant response to treatments can be achieved. This challenge has intensified in recent years as emphasis has increased on multiresource planning and on concurrent demand for cost/benefit information. We can no longer be content with understanding the response of succession to a few natural disturbances in a narrow range of conditions during a short period.

Timber researchers are already developing multiple-product yield tables (Bennett and Clutter 1968). Multiresource model builders are asking us for response curves and coefficients for range and wildlife habitat over a broader area than that for which we can currently provide answers.

In the past, wildlife and range managers have accepted the secondary role of their products in relation to timber. Much of our past research and some of our present research is based on this role. In most management situations, range and wildlife will continue to play such a secondary role, and we should recognize this restriction in our ecological studies. However, there is growing recognition that considerable acreage exists where timber should be of secondary importance. Have we the ecological base to maximize range or wildlife habitat on such sites if we are given the opportunity? There is the dual challenge, then, to optimize individual resources as well as multiple resources. Such planning requires a broader ecological base than we have provided in the past.

AN INTEGRATED MANAGEMENT APPROACH

Where do our current research programs stand in relation to this challenge? Our range project in the pine-wiregrass type has been reorganized into an integrated range-timber-wildlife project (Duvall and Hilmon 1965). We were in fair condition in relation to understanding response of range—from a cattle-grazing standpoint—to major disturbance factors: Fire, cattle, timber etc. However, even here, the breadth of our knowledge is inadequate. For example, we had studied fire effects intensively where fire was applied in the late fall or winter (Hilmon and Hughes 1966). We have little information on community response to burning at other times of the year. Our primary emphasis now is to provide some knowledge of community response to a wide range of alternative treatments. Our knowledge of wildlife habitat response to even the major factors over a narrow range is limited or inadequate. We have increased emphasis on habitat research, especially of the interrelations of habitat research with range and timber. We are in the very early stages of developing models to optimize forest range productivity in this type.

AUTECOLOGICAL STUDIES

Research to define the ecological amplitudes of key species has been accelerated. Initial autecological studies of the principal shrub, *Serenoa repens* (Hilmon 1968), and the principal wiregrass, *Aristida stricta* (Parrott 1967), have been completed. Studies of key wildlife food plants *Cassia fasciculata* (Cushwa et al. 1968) and *Vitis aestivalis* have been started. Southern Forest Experiment Station range scientists are studying autecology of pinehill bluestem (*Andropogon divergens*) and of longleaf uniola (*Uniola sessiliflora*). Intensive study of the phenology of principal deer browse plants is also underway.

We are expanding cooperative research started at Tifton, Ga., in order to better define tree and understory response to intensive management (Hughes et al. 1966). Species adaptability and community ecology in response to fertilization, cultivation, and other intensive culture is a special challenge of range ecology and one we have neglected in the past.

WILDLIFE HABITAT

Our wildlife habitat research in the southern Appalachians is about where coastal range ecology was 20 to 25 years ago. Specific habitats used by the principal game species, seasonal use of forage plants, nutritive content of plants, and similar data generally are lacking for the mountains. Meanwhile, biologists are under pressure to (1) predict impacts of various land management treatments on habitat and (2) to improve habitat capacity. Wildlife habitat research is just passing from the phase where it closely followed current management problems to where it is beginning to develop an ecological base on which to prescribe optimum management. Current management problems

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—such as effects of clearcutting—are serious, and some effort in immediate applied research is necessary. However, as experience with browse surveys indicated, a more complete definition of understory ecology is essential.

Browse surveys, using timber survey plots, were made on at least eight southern National Forests and related areas (for example, see Moore 1967). Recent analyses of stomach contents of 490 deer indicate that woody twig ends constitute less than 1 percent of total contents during the critical winter period (Cushwa et al. 1969). We know little about the ecology of plants and plant parts which were eaten—herbs, fruits, mushrooms.

We have some data for a 10-year period on plant succession following clearcutting and on adjacent uncut areas (Harlow and Downing 1969). However, only recently have we concentrated on defining the succession of a broader array of plant groups than woody browse. Now another aspect—the nongame wildlife, especially songbirds—is growing in importance. Knowledge of the condition of woody species above $4\frac{1}{2}$ to 5 feet would be an asset. Special studies of this stratum and the overstory must be made to determine optimum conditions for songbirds (Hooper and Crawford 1969).

These examples emphasize the need for fuller descriptions of plant communities and their succession, not only in range but in wildlife as well.

THE ECOLOGICAL SET AND MULTIRESOURCE MANAGEMENT

I mentioned earlier our start on models to integrate cattle-timber-wildlife management in the coastal pine-wiregrass type. We have developed a proposal to optimize wildlife, water, timber, and recreation benefits on a 14,000-acre management area in North Carolina. This proposal presents the concept of management by ecological set, an idea defined initially by T. H. Ripley and D. O. Yandle (1969). The ecological set is a management unit large enough to provide sustained yield of all products considered in a multiresource mix. For example, if the home range of a deer is 500 acres, the ecological set must contain this acreage; and treatments, such as a cutting system, must be applied in such a way that they provide a continuous supply of forage. Otherwise, optimum production of deer cannot be achieved in modeling multiresource production.

National Forest financing has enabled us to hire a Duke University statistician-economist to develop preliminary models for multiresource production on this area. The questions he is asking on input data embarrass not only the range ecologist but the silviculturist and watershed specialist as well.

THE PIEDMONT CHALLENGE

The Piedmont Province is an extensive area where relatively little work on range ecology has been done, and an area where the potential for wildlife, in particular, is great. The Southern Forest Experiment Station has one range scientist assigned to loblolly-shortleaf range problems. Their wildlife project is studying deer habitat problems in the type. The Southeastern Forest Experiment Station wildlife project is devoting about 3 man-months to this area, primarily on quail and turkey habitat. University ecologists have described old-field succession in this type (Oosting 1942); effort has been concentrated on the early stages. Opportunities to modify succession by management for resources other than timber have received little attention.

CENTERS OF RANGE ECOLOGY

There are no non-Forest Service centers of range ecology in the South except for Texas A & M. Universities and State Game Departments have concentrated on animal ecology, research which is an essential complement to our habitat research.

Four major ecological centers at universities—Duke, Georgia, Emory, and Tennessee—are not concentrating on problems with immediate range and wildlife management application. We have received major assistance from Duke and Virginia Polytechnic Institute on autecological studies and from Florida on quail habitat research. One private company has a full-time wildlife biologist devoting most of his time to habitat research. The Bioscience Department at Florida State, and Tall Timbers—a private research station—are cooperating in an ecological study of the northern tier of counties in western Florida. Their descriptions of communities, definitions of successional sequence, and identifications of factors responsible for formation of these communities should interest range ecologists. We are developing cooperation with the Institute of Ecology at Georgia. Their emphasis on ecosystem productivity closely parallels our needs in multiresource management research.

In summary then, the status of range ecology in the South is one of transition. We are moving rapidly into the era where emphasis is on ecology in a broad sense, and it is likely that various functional aspects of ecology will be deemphasized even more in the future.

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An Ecological Classification Proposal and its Importance in Land Measurement

F. C. HALL[1]

The two classification systems for American vegetation have opposing philosophies: Polyclimax community grouping (Daubenmire 1952) and the continuum (Bray and Curtis 1957). These philosophies will be briefly discussed in relation to a proposed climax continuum philosophy.

PHILOSPHIES

Polyclimax.—The polyclimax concept states that various combinations of soil, topography, and climate create numerous environments. Within each environment, a plant community will eventually maintain itself in a reasonably stable state (climax) if some part of the environment does not change. Also, plant species tend to be naturally grouped according to their similar ecologic amplitudes; therefore, plant communities tend to be repeatable within a geographic area. Consequently, these various climax plant communities may be classified into groups called habitat types or plant associations. Thus, these associations may then be considered a reflection of the environment (Daubenmire 1955).

Classification is generally accomplished as follows: First, a study area is thoroughly evaluated for climax vegetation using reconnaissance techniques. Next, the plant communities are classified into habitat types or associations. Then, modal climax plant communities representing each association are intensively sampled. Selection of these modal communities is based on the observer's opinion of how well they represent an association. As a result, polyclimax community grouping produces habitat types or associations described according to modal qualities. The classification recognizes variation within modes, transitions between modes, and ecotones between plant communities where the environment changes abruptly.

Continuum.—The concept of climax is seldom applied or considered in this philosophy. The continuum philosophy states that no two plant species have exactly the same ecologic amplitude; rather, each species has its own unique amplitude. Soils, topography, and climate tend to occur in continually variable combinations. Interactions of environments and different plant amplitudes produce continually variable plant communities which do not repeat themselves throughout the landscape. Thus, plant communities cannot be classified into groups (Bray and Curtis 1957).

Classification is generally accomplished by sampling any stand that does not exhibit obvious, recent disturbance. As a result, both successional and climax vegetation are often included in the data and the classification. Continua in successional vegetation have been clearly demonstrated in range, wildlife, and timber management. For instance, one kind of successional pattern in species dominance and composition will occur if a plant community is overgrazed by cattle; the same plant community will exhibit a different successional pattern if overgrazed by sheep; a still different successional pattern will be evident if the community is overgrazed by elk; and a foruth successional pattern might characterize overgrazing by deer. Thus, many successional continua are possible for a given climax community. If these successional gradients are indiscriminately combined with climax vegetation, a continuum ordination of existing vegetation is imperative. The need for such an ordination may be the most severe objection to present application of continuum philosophy.

PROPOSAL: CONTINUUM IN CLIMAX

A modification of both philosophies is proposed, that of a continuum in climax vegetation which is characterized by acceptance of the following: (1) The climax concept; (2) continuum tendencies in climate, soils, and geomorphology; and (3) differences in ecologic amplitudes of plant species. Several qualifications distinguish this concept from the continuum concept. First, separation of climax and seral continuum gradients is essential for such management problems as range condition and trend evaluation, silvicultural guides, and field application of research results. Second, abrupt changes in environment will result in abrupt changes in plant communities. Third, "complete continua gradients" may not always exist; indeed, they may seldom exist in the mountainous West.

The following examples should clarify the climax continuum philosophy. Slope exposure continua may be illustrated using a conical hill (such as a cinder cone). Vegetation on the south slope might be *Agropyron/Poa,* which changes abruptly at the crest to the north slope *Festuca/Agropyron.* As one moves from midsouth slope on the contour toward midnorth slope, he should encounter a continuum gradient where the two plant communities, soils, and microclimates intergrade. This "conical hill" is seldom encountered; however, an

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analogous situation does occur in meandering canyons which have slopes facing any direction of the compass. It is on these areas that slope direction continua are expressed. A second continuum gradient may occur as slopes vary from 0 to 100 percent. A third reflects changes from the bottom of a long slope to the top, which may be the result of microclimatic changes and soil drainage differences. A fourth gradient occurs with changes in soil properties, and a fifth occurs with changes in local climate even though topography and soils remain reasonably constant. The list could be greatly expanded, particularly when various factors interact, creating an almost infinite variety of continuum gradients.

Reasons for the proposal.—In 1956, I used the polyclimax community philosophy in developing tentative range condition guides for one ranger district where application was quite successful. However, since then, I have mapped and analyzed range condition on approximately 1 million acres in the Blue Mountains of central and northeastern Oregon. Experience on these 1 million acres clearly demonstrated continua in environment and the inappropriateness of condition guides based upon modal community groups developed in a limited geographical location. In fact, using these guides approximately two-thirds of the land area could not be suitably rated for condition.

Thus, range condition guides or other vegetation management guides based on the modal concept of community groups can lead to misinterpretation of site potentials, application of management practices not particularly appropriate to many sites, and erroneous mapping when based on site potential or range condition. Since the land manager is responsible for managing each acre under his jurisdicition, guides must be developed and written which are applicable to as much land area as possible. They must be understandable and acceptable to field personnel. They must be developed for polyclimax "transition zones" or "intergrades" as well as for modal conditions—which is another way of suggesting guides based upon continuum gradients.

I have also installed 50 to 75 three-step clusters and have reread an 100 more as part of range allotment analysis. These clusters are located in areas heavily used by livestock and thus provide a measure of animal effects on the range. Cluster location is further qualified by placement in range types reasonably similar to major kinds of vegetation in the allotment. Unfortunately, livestock care not for modal conditions representing community groups, and allotment or district boundaries are not located around modal conditions. As a result, many three-step clusters used for administrative purposes are not placed in modal sites. Polyclimax community group condition guides are seriously deficient in estimating range condition, interpreting trend, and appraising management alternatives on these cluster locations. Too often, environmental factors measured at cluster locations were significantly different from those suggested by community group guides.

Repeatble climax communities mean repeatable environments. Yet climatologists have demonstrated the variability of climatic gradients such as decreasing temperature with elevation, increasing precipitation with elevation on windward mountain slopes, and decreasing precipitation on leeward slopes. Geomorphologists have demonstrated continuous variability in landform from the steepest mountains to the flattest lakebeds. Soil scientists have conceded continuum in soils for years and have employed soil taxonomists (regional or State soil coordinators) to reconcile classification and to name soils within this variability. How, then, can repeatable, effective environments be formed from continuous variability in all the factors which make up the environment?

No literature has been found which supports the contention that different plant species have similar ecologic amplitudes. Daubenmire's (1952) Table 1 (page 304) was used to plot the ecologic amplitudes of 19 species according to the two-dimensional concept proposed by Curtis and McIntosh (1951). Considerable difficulty was encountered in delineating the associations according ecologic amplitudes of species. If species have different ecological amplitudes and if there is continual variability in factors which make up environment, how can there be repeatable climax plant communities which can be classified into groups suitable for mapping or land management?

Finally, the author, using multivariate analysis, found continuum tendencies within and between community groups in a study of the 5-million-acre Blue Mountain landmass in central and northeastern Oregon.

Importance of the climax continuum philosophy in ecology and land management. —Range condition guides based upon modal plant community groups are generally inappropriate because actual site potentials within the plant association vary considerably and because transition areas are ignored. Regarding varience, some areas have a potential for reaching only high-fair condition, while other areas have a potential somewhere above excellent when the modal is considered excellent. This variability on condition guides must be recognized and must be designed so that range condition can be satisfactorily rated on most of the site potentials within a geographic area.

Trend evaluation is customarily associated with condition evaluation. However, a very important distinction must be noted. Trend is evaluated on a specific site, a site which has its own unique enironment. Condition guides, on the other hand, are based upon sampling many sites from which numerical data are statistically evaluated. Thus, condition guides are mathematical abstractions representing only averages of site characteristics and modal environment potentials—they are not a true measure of actual condition or potential on a specific site. The use of condition guides in trend interpretation must be limited to *suggesting* site potential and *approximating* range condition as a guide for assuming that upward trend is possible or that downward trend has occurred. The guides should not be used as a measure of trend because they cannot measure a specific site. Since each site may be considered as some point in a continuum gradient, condition guides based upon such a gradient will more accurately evaluate specific sites.

Management practices can and are classified as a means for discussing their merits, limitations, and applicability in vegetation manipulation. Plant communities may be classified in any manner that will meet our objectives, whether they be for land management, demonstration of continuum gradients, maps of similar site potentials, or descriptions of modal environments. In land management, plant communities should probably be grouped according to similarities and limitations in management practices, productivity, and numerical simILairty of important characteristics. A single classification may not meet all these criteria. For example, the numbers of three-step "hits" and percent composition of decreasers and increasers may be similar for two classification groups, such as *Agropyron* on steep slopes and *Artemisia tridentata/Agropyron* on moderate slopes. Both can be evaluated with the same condition guide and could be grouped together; however, managment is different due to the presence or absence of *Artemisia*.

Mapping also requires grouping of plant communities for efficiency and simplicity. Since mapping objectives in land management are directly related to resource management, plant communities should be classified according to significant differences in management characteristics. For example, *Agropyron/Festuca* on moderate slopes may be divided into shallow and deep soil groups to reflect differences in forage production, revegetation potential, and sensitivity to grazing. In range mapping, each map unit must be rated for condition. In this way, the land manager obtains a picture (map) and an inventory of areas differing significantly in management requirements and limitations. However, he must understand that map units and inventory lists are largely generalized approximations; they may not represent real biological entities or actual site potentials and characteristics.

Sampling will often be influenced by the climax continuum philosophy. All studies evaluating plant community distribution or species distribution should be designed to sample continuum gradients. If gradients occur, this sampling will tend to more realistically evaluate the situation as it occurs in the field. If gradients do not occur, the sampling will clearly indicate grouping or clustering of similar plant communities. Sampling limited to a few thousand acres will often indicate grouping or clustering. Samples of vegetation over hundreds of miles in all directions are required for good gradient expression.

Interpretation of research findings is influenced by this philosophy. Study results often are applicable only to certain portions of a continuum gradient. These results generally will be less and less applicable as distance from the study site increases and as different plant communities are encountered. Suggestions of gross similarities in vegetation, such as a "juniper zone," tend to be misleading because they imply some kind of uniformity in vegetation and environment. Such broad distributions often reflect the ecological amplitude of a species. Most species, such as juniper, occur over wide areas encompassing part of a State or several States. Such breadth of amplitude encompasses great variability in environment and is not a suitable basis for plant community classification that is useful in vegetation management.

AN EXAMPLE OF CONTINUUM IN CLIMAX

Variability of community groups.—The 5 million-acre Blue Mountain landmass in central and northeastern Oregon was evaluated by intensive ecological reconnaissance. Using the climax continuum philosophy, 450 sample locations were selected. Only locations free or nearly free of disturbance by grazing or logging were selected. Herbaceous vegetation was sampled using the modified three-step method (Parker and Harris 1959). Study objectives were to develop range condition guides and to develop or to improve vegetation management guides. One method used to accomplish these objectives was classification of plant communities based upon characteristics important in management. Table 1 shows the mean and standard error for hits and for composition of three species and two groups of species, decreasers and increasers, for five nonforest plant

TABLE 1.—*Mean and standard error of hits and composition for species or groups of species in five nonforest range types*

	Agsp shallow	Agsp deep	Agsp steep	Arar agsp	Artr agsp
Hits on:					
Poa secunda	7±5	9±5	3±1.5	4±3	5±2
Agropyron	7±4	8±4	8±4	9±3	6±6
Festuca	2±2	5±3	4±3	3±3	7±6
Composition of:					
Poa secunda	40±15	35±14	19±12	33±14	25±7
Agropyron	24±12	22±14	36±11	29±14	30±27
Festuca	8±9	28±13	22±14	13±13	28±23
Hits on:					
Decreasers	9±4	13±5	12±4	14±6	16±4
Increasers	9±4	10±5	4±4	5±3	6±3
Composition of:					
Decreasers	32±11	48±12	51±13	44±11	58±9
Increasers	42±14	37±13	25±15	38±13	30±9

community groups. This table was used as a basis for formulating condition guides, based on hits and composition of species and species groups, for each plant community group. Standard errors vary from 25 to 100 percent of the mean for hits and from 15 to 100 percent of the mean for composition. Lowest standard errors were obtained by combining plant species into classifications of decreasers and increasers.

Wide standard errors within groups reflect vegetation variability resulting from continuum gradient sampling. These illustrate the problems encountered in classifying community groups within a gradient by attempting to apply the modal group concept to field conditions. Variability exceeds one condition class (±10 percent of the mean), suggesting that five condition classes cannot be justified statistically. Therfore, four condition classes were utilized. Very poor condition was defined as one lacking in decreaser plants and so deteriorated that adjustment in livestock management is generally not an economically feasible method for improving range condition. Three condition classes were based upon presence of decreaser vegetation: Good represents 66 to 100 percent of "possible" hits and composition; fair, 33 to 66 percent; and poor, 2 to 33 percent.

Condition could be more accurately evaluated by division into finer groups. However, criteria for field identification of these finer groups in poor and very poor condition were difficult to describe. Vegetation indicators are generally obliterated, and no single site factor could be used. Accurate site identification would require measuring several environmental factors. These factors, when entered into a multiple-variate analysis formula, could be used with much greater accuracy in suggesting potential vegetation than as indicators of a plant community group or association.

Multiple-variate analysis and the continuum.—Sampling data were analyzed by multiple-variate analysis. Plant community types, a name assigned to community groups based upon similar management characteristics, were evaluated individually. Also, community types with generally similar vegetation were grouped and analyzed for continuum gradients. Dependent variables included hits and composition by species and by groups of species, forage production, and surface stoniness. Thirty-two independent variables were tested.

Table 2 lists environmental factors significantly associated (5 percent level) with hits and composition of *Agropyron spicatum, Festuca idahoensis,* and *Poa secuda;* total herbage production; and surface stoniness in the *Agropyron/Poa* community type. The analyses accounted for 40 to 71 percent of the variability. No single factor is predominantly associated with all items or with any particular item, suggesting multiple-factor continuum tendencies and independent ecologic amplitudes. In many cases, factor associated with a species' hits is not always associated with that same species' composition because composition is associated with other dependent variables. For example, elevation is negatively correlated with *Agropyron* hits but is not associated with *Agropyron* composition. In six of eight cases, factors other than soil characterists account for most of the variability.

Table 3 shows factors associated with vegetation when four nonforest bunchgrass community types were combined for analysis. In this case, the characteristics of soils account for more of the variability than do topographic or climatic factors, suggesting that soils were apparently reflected in community-type classification. Different factors are associated with a species' hits and composition when community types are grouped. What, then, are the "real" factors associated with a species' distribution?

TABLE 2.—*Topographic, soil, and soil surface factors analyzed for association with vegetation and surface stoniness in the Agropyron/Poa type*

	Dependent factor, percent variation accounted for							
	Agropyron		*Festuca*		*Poa*			
Independent factor	Hits	Comp.	Hits	Comp.	Hits	Comp.	Total production	Surface stone
Topography:								
Elevation	12	----	22	31	----	21	----	6
Percent slope	----	----	----	----	40	----	----	38
Slope direction	----	----	16	10	8	13	----	----
Slope position	----	21	8	----	----	----	----	----
Microrelief	----	14	----	6	----	----	7	----
Range east	----	----	----	----	----	----	----	----
Township south	----	----	----	----	----	----	----	----
Soil:								
A pH	----	----	----	----	----	----	----	----
A texture	----	----	----	10	----	----	----	----
A structure	----	----	----	----	----	----	----	----
A stone	----	----	----	----	----	----	----	----
A depth	----	----	----	----	----	----	----	----
A color	----	----	----	----	----	----	----	----
B pH	----	----	----	----	----	----	----	----
B texture	----	----	----	----	----	----	----	----
B structure	----	----	----	----	----	----	----	----
B stone	----	----	----	----	----	----	----	----
B depth	----	----	----	----	----	----	----	----
B color	----	----	----	8	----	----	9	----
C pH	----	----	----	----	----	----	----	----
C texture	----	----	----	----	----	----	----	----
C stone	----	----	----	----	----	----	----	----
C depth	----	----	----	----	----	----	----	----
Total depth	28	----	----	----	6	37	----	22
Effective depth	----	----	----	----	----	----	45	----
Soil stone	----	20	----	----	----	----	----	----
Bedrock fracture	----	----	----	----	----	----	----	----
Surface:								
Rock	----	----	----	----	----	----	----	(1)
Bare ground	----	----	----	----	----	----	16	(1)
Erosion pavement	----	----	----	----	----	----	----	(1)
Litter	----	----	----	----	----	----	----	(1)
Moss	----	----	----	----	----	----	----	(1)
Total variability accounted for	40	55	46	65	54	71	77	66

[1] Indicates these items not tested.

Multiple-variant analysis again demonstrates continuum tendencies between grouped plant communities. With the exception of hits on *Poa*, the analysis accounted for 43 to 74 percent of the variability.

Table 4 compares factors associated with *Agropyron* composition in six community types. The analysis accounted for 45 to 92 percent of the variability and suggested differences in continuum gradient expression. Within community types, nonsoils environmental characteristics generally account for more of the variability in composition. Of particular interest, however, is the lack of consistency in factors affecting *Agropyron*. No single factor was important in more than half of the community types. Since each community type has its own set of factors influencing continuum gradients, the presence of each type would seem to indicate different environments. This finding lends some credence to classification of plant communities. The real questions are whether climax plant communities tend to be clustered within a continuum gradient, whether clustering reflects the investigator's subjective determination of sample location, or whether complete gradient expression is possible in a landmass largely isolated within a grass and sagebrush steppe.

These tables clearly demonstrate that plant communities or vegetational patterns cannot be evaluated by single-factor analysis. In nearly every community type, three or more factors had a significant effect on vegetation variability. Since (1) several factors are important within a community type and (2) since these factors are not universally important between community types, identification of environments (climax communities) in the field under distrubed conditions presents some challenging and complex problems. One procedure under investigation is the classification of plant com-

munities into community types based upon similarities in management and easily distinguishable field characteristics. Potential vegetation could then evaluated within community types by use of multiple-variate analysis formulas in which the investigator would measure prescribed environmental factors for use in the formula. For example, potential hits on *Poa secunda* in the *Agropyron/Poa* type would require measurement of: Percent slope, slope direction, and total soil depth. These measurements would be entered in the following formula: *Poa* hit $= 21.30 - 0.11$ (percent slope) -0.31 (slope direction) -0.14 (total soil depth).

TABLE 3.—*Topographic, soil, and soil surface factors associated with vegetation and surface stoniness when four nonforest bunchgrass types are combined for analysis* (*Artemisia arbuscula, A. rigida, A. tridentata, and Agropyron/Poa*)

	Dependent factor, percent variation accounted for							
	Agropyron		Festuca		Poa			
Independent	Hits	Comp.	Hits	Comp.	Hits	Comp.	Total production	Surface stone
Topographic:								
Elevation	----	----	----	----	----	11	----	----
Percent slope	----	----	----	----	----	----	----	----
Slope direction	14	16	11	13	----	----	6	----
Slope position	----	----	----	----	----	----	----	----
Microrelief	----	----	----	9	----	----	----	----
Range east	----	----	10	5	----	----	5	7
Township south	15	18	----	----	----	----	----	----
Soil:								
A pH	----	----	----	----	----	----	----	----
A texture	----	----	----	----	----	----	----	----
A structure	----	----	----	----	----	----	----	----
A stone	----	----	----	----	----	7	----	----
A depth	----	----	----	----	----	6	----	7
A color	----	----	----	----	----	----	----	----
B pH	6	----	----	----	----	----	----	----
B texture	----	----	----	----	----	----	----	----
B structure	----	----	----	----	----	----	----	----
B stone	8	----	----	----	----	----	----	----
B depth	----	----	----		----	----	----	----
B color	----	----	----					
C pH	----	----	----	----	----	----	----	----
C texture	----	----	----	----	----	----	----	----
C stone	----	----	----	----	----	----	----	----
C depth	----	----	----	----	----	----	----	----
Total depth	----	9	----	----	----	26	----	----
Effective depth	----	----	37	41	----	----	18	31
Soil stone	----	----	----	----	----	----	----	5
Bedrock fract.	----	----	----	6	----	----	----	----
Surface:								
Rock	----	----	----	----	----	----	----	[1]
Bare ground	----	----	----	----	----			[1]
Erosion pavement	----	----	----	----	----	----	----	[1]
Litter	----	----	----	----	----	----	----	[1]
Moss	----	----	----	----	----	----	----	[1]
Total variability accounted for	43	43	58	74	0	50	29	55

[1] Indicates these items not tested.

TABLE 4.—*Variation in factors associated with Agropyron composition*

Independent factor	Range types, percent variation accounted for					
	Artemisia rigida	Artemisia arbuscula	Artemisia tridentata	Agropyron/ Poa	Pinus Agropyron	Pinus Festuca
Topography:						
Elevation	----	23	----	----	----	----
Percent slope	50	----	----	----	13	----
Slope direction	----	----	45	----	----	22
Slope position	----	16	----	21	----	28
Microrelief	----	----	----	14	----	5
Range east	----	----	----	----	----	----
Township south	----	----	----	----	----	----
Soil:						
A pH	----	----	----	----	----	----
A texture	----	----	----	----	----	----
A stone	10	----	----	----	----	----
A depth	----	----	----	----	----	5
A color	----	----	----	----	----	----
B pH	----	----	----	----	----	----
B texture	----	----	----	----	----	----
B structure	11	----	----	----	----	----
B stone	----	----	----	----	44	----
B depth	----	----	----	----	----	----
B color	----	----	----	----	----	16
C pH	----	----	----	----	----	----
C texture	----	----	----	----	----	----
C stone	----	----	----	----	----	----
C depth	----	----	----	----	24	----
Total depth	----	23	----	----	----	16
Effective depth	11	----	----	----	----	----
Soil stone	----	----	----	20	----	----
Bedrock fract.	----	----	----	----	----	----
Surface:						
Rock	----	----	----	----	----	----
Bare ground	----	----	----	----	----	----
Erosion pavement	----	----	----	----	----	----
Litter	----	----	----	----	----	----
Moss	----	----	----	----	----	----
Total variability accounted for	82	62	45	55	81	92

SUMMARY

The classification philosophies of polyclimax community groups and continuum gradients have been discussed. A continuum in climax vegetation is proposed. This philosophy recognizes: (1) The climax concept, (2) plant species have independent and different ecological amplitudes, (3) climate, geomorphology, and soils tend to occur in continuum gradients, (4) climax communities tend to be continually variable, (5) abrupt changes in the environment are refelcted in abrupt changes in plant communities, (6) sampling should reflect continuum tendencies, and(7) plant communities can be grouped in any manner suitable to meet stated objectives.

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Use of Ecological Knowledge to Improve Big-Game Range

JACK E. SCHMAUTZ [1]

The Forest Service goal in big-game habitat management in northern Idaho and western Montana is to maintain and to improve existing and potential game winter range by any feasible and practical method available. Much emperical evidence and some research data show controlled fire and various silvicultural practices can be important tools in the renovation and improvement of declining game ranges.

FIRE

Uncontrolled fire was once an important element in the forest environment of the northern Rockies. Most of the big-game ranges in northern Idaho and western Montana were created by fire. In the quarter century from 1910-1934, more than 6.25 million acres were burned by wildfire. Since then, however, the acreage burned has declined steadily. There have been occasional fire years such as 1961 (when 63,000 acres were burned) and 1967 (when 83,000 acres were seared by wildfire). Such acreages are small, however, when compared to the 2.7 million acres burned in 1910 and 1.5 million acres burned in 1919.[2]

The initial effects of these large burns were disastrous to trees and to watersheds, but the burned lands were quickly revegetated by shrubs. Some of the burned area developed into highly productive game range. Now forage production is declining: Partly because the forest has reclamimed its own, partly because the shrubs have grown out of reach of the deer and elk, and partly because many palatable shrubs have become decadent through over use.

Because of its unpredictability and its potentially disastrous consequences, wildfire cannot be seriously considered in big-game habitat management. However, controlled burning can be used to improve wildlife habitat. Planned burning in April and May to renovate northern Idaho game ranges has been quite successful on *Pseudotsuga-Physocarpus*, *Thuja-Pachistima*, and *Abies grandis-Paschistima* habitat types, and, to a lesser degree, on *Tsuga-Pachistima* (Habitat types described by Daubenmire 1952, 1966. No damage to soils and watersheds has been noted, even on slopes as steep as 40 to 50 percent. All shrub species present have sprouted quickly, and the slopes were revegetated in a few weeks. *Salix scouleri* and *Acer glabrum*, both palatable shrubs, sprouted especially profusely.

On the other hand, burning in the various *Abies lasiocarpa* associations has not been so successful. Resulting understory shrubs are not particularly palatable to deer and elk. Also, subalpine fir associations generally do not occur on key winter ranges.

Fire, under certain circumstances, can also be used to change the composition of shrub stands. A palatable species may be virtually absent in a shrub stand, but its seed may be present and viable in the duff or mineral soil. Fire may induce germination. Such is often the case with *Ceanothus* in the *Pseudotsuga-Physocarpus* habitat type. Gratkowski (1962) and Lyon (1966) have shown that seed of *Ceanothus velutinus* remains viable in the duff for many decades and that heat in excess of 140°F. followed by a cold period is necessary for successful germination. Some good *Ceanothus* stands have been obtained by burning. For example, 2 years after a controlled August burn on a 120-acre stand of mature Douglas-fir on the Sawtooth Forest in central Idaho, Lyon (1966) recorded three to five well-distributed, seedlings per square foot, Prior to the burn, despite an intensive search, only one *Ceanothus* plant was found on the area.

Studies of Lyon and Stickney (1966) have shown sites on which prescribed burning can be used successfully can be recognized if four conditions should exist:

1. Shrub crown volume should be high. In general, the greater the crown volume, the greater is current production and the more rapid is the potential recovery rate.
2. Species composition should indicate a potential for success. The species present should be palatable to game and should have a high sprouting vigor following burning.
3. If a poor potential recovery is indicated by inadequate crown volume and presence of unpalatable species, soil and duff samples may show the presence of stored seed of more desirable species (e.g., *Ceanothus*).
4. Potential erodibility of the soil must be determined. High erodibility will not preclude the use of fire but will dictate greater care in planning and in burning.

In addition to the above, we need to know how the various shrub species respond to different fire intensities at different times of the year and with different frequencies of applica-

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[2] Statistics are from the Division of Fire Control, USDA Forest Service, Region 1, Missoula, Mont.

tion. When we have obtained this knowledge, existing shrub stands may be intelligently manipulated with fire to achieve desired composition and production.

SILVICULTURAL METHODS

Logging and related silvicultural treatments can be used to improve key winter range. Numerous authors have reported that almost any amount of reduction in tree canopy increases the understory and subsequent use by big game. (Pase 1958; Pengelly 1963; Reynolds 1962, 1966a, 1966b; and Young et al. 1967.)

Thinning dense stands of young lodgepole or larch can also increase the production of declining understory shrub stands. On the Flathead National Forest in western Montana, strip thinning with a brush chopper increased production of available palatable browse by 27 percent the first year. Greater shrub growth is expected in the second year after treatment. The economic worth of the additional browse for white-tailed deer the first year was calculated at $1.07 per acre. The cost of thinning was $15.22 per acre. The silvicultural values alone are estimated to yield about 8.9 percent on the investment. With wildlife values added, about a 10.8 percent return on the investment is expected (Evans 1968).

As with fire, if we know the existing shrub crown volume, species composition, and species reaction to treatment, we can predict the probable success of silvicultural treatments in improving game range. We should also know how long the benefits of the treatments can be expected to last. Quantitative data by years and habitat types are needed to properly coordinate timber management programs with the needs of wildlife habitat management.

SUMMARY

Controlled fire and silvicultural treatments can be used to improve big-game ranges. Prerequisite information needed to predict probable success of the treatments on various sites include:

1. Estimates of existing volume of shrub crowns as a measure of current production and potential recovery rate.
2. Species composition and knowledge of species reaction to treatment.
3. Indications of seed of desirable shrubs stored in the duff and upper layers of mineral soil.
4. Knowledge of the erodibility of the soil.

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A Model to Incorporate Soil Survey and Allotment Analysis Data into Range Management Planning

JACK E. SCHMAUTZ [1]

Range allotment analyses and soil surveys have been completed on many livestock allotments on National Forest ranges in northeastern Washington, northern Idaho, Montana, North Dakota, and northeastern South Dakota. The maps and large amount of data that have been obtained from these analyses and surveys are quite confusing to most land managers. The problem is: How can this information be summarized and integrated into a usable working tool for the resource manager?

A model has been developed to incorporate soil survey and allotment analysis data into range management planning.[2] The basic information used in the model was obtained from a detailed soil survey [3] and from the range analysis of the Cow Creek Allotment, Ashland Ranger District, Custer National Forest, southeastern Montana.

The range allotment analysis was made according to current Forest Service regional standards.[4] Soils were mapped to the series level, and mapping units were based on slope, salinity, and erosion phases.

THE MODEL—WHAT IT IS

The model for the Cow Creek Allotment consists of:

1. A base soils map on which the soil series have been classified into five productive potential classes.
2. Transparent overlays showing:

   a. Soils classified into four potential erosion hazard classes.

   b. The allotment classified according to (1) range condition class, (2) trend in condition, and (3) primary and secondary range.
3. A table in which the soils were rated as to their probable response or suitability to desired cultural or management practices.

STEPS IN MAKING THE MODEL

1. Soils were classed into five productive potential classes.

   a. Clipping studies to estimate production potential were made on modal soils on ranges judged to be in good or excellent condition. These soils were grouped into five production classes, with the lowest class producing 400 pounds or less of forage per acre and the highest yielding 875 pounds or more.

   b. No ranges in good condition could be found for some soils. Productivity potentials of these soils were extrapolated from soils for which clipping data were available. Soils with similar physical and chemical characteristics were judged to have similar productive potentials and were classed accordingly. Physical characteristics considered were: Thickness, texture, structure, infiltration, and porosity. Chemical characteristics used were: Cation exchange capacity, pH, base saturation, C:N ratios, and organic matter content. Data for these characteristics were obtained from the soil survey.

   c. The productive potential classes were colored on a base soils map with a scale of 2 inches for each mile.

2. Soils were subjectively classified into four potential erosion hazard classes.

   a. Potential erosion hazard classes ranged from moderate to very high. The classification was based entirely upon soil characteristics and was independent of vegetation; as a result, the confounding effects of range condition were eliminated. Factors considered in evaluating the potential erosion hazard of a soil included soil thickness, structure, texture, size and strength of the peds, and rates of infiltration and percolation.

   b. A colored transparent erosion hazard overlay was made to the same scale as the base map.

3. A colored transparent overlay was made showing range condition and trend and primary and secondary range.

Ranges were classified into condition and trend classes and as primary or secondary

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[2] Developed jointly by Richlen, E. M., Division of Soils and Watershed Management, Region 1, USDA Forest Service, Missoula, Mont.; Almen, C. E., Colville National Forest, Colville, Wash.; Smith, H. O., Custer National Forest, Billings, Mont.; and the author.

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[4] Allotment analysis instructions and standards and given in Forest Service Handbook 2209.21 R1, Range Environmental Analysis Handbook.

ranges according to Forest Service standards and criteria.[5]

4. Soils were rated as to their probable or expected response or suitability to a number of desired cultural or management practices.

a. Practices considered were: Potential fertilizer response; suitability for terracing, pitting, water impoundments, plowing and seeding, and deep furrow drilling; and probable response to plant control, interseeding, and intensive management systems.

b. Ratings and recommendations for these practices were tabulated by soil mapping units. The ratings and recommendations for each unit were explained in notes appended to the table.

HOW THE MODEL HAS BEEN USED

The range analysis showed a large acreage of secondary range in good condition on the Cow Creek Allotment. A portion of the secondary range was on soils with a high production potential and with a relatively low erosion hazard. This part of the secondary range can be safely developed into primary range. Another part of the secondary range was occupied by low-producing soils with very high erosion hazards. This part should not be converted into primary range.

The proper location of fences has been facilitated. The allotment management plan called for an intensive management system with several pastures. As originally planned, one pasture cross-fence would have intersected the boundary fence on a soil with a very high erosion hazard. Because livestock often congregate in fence corners, sorespots would probably develop soon. The fence location was changed so that the intersection was on soils with a much lower erosion hazard.

The model has also been used to estimate probable response of an area to sagebrush control by herbicides. Potential productions of palatable forage were estimated, and likely problem areas were pinpointed.

[5] Standards and criteria for range condition and trend classes and for primary and secondary range are given in FSH 2209.21 R1, Range Environmental Analysis Handbook.

SUMMARY

A model has been developed to integrate data from soil surveys and range allotment analyses into a simple, useful tool for planning by the resource manager. The method consists of classifying soils into production and potential erosion hazard classes, mapping ranges by condition classes, and classifying them as primary or secondary range. Soil mapping units are then rated as to probable response to certain cultural and management practices.

☆ U.S. GOVERNMENT PRINTING OFFICE: 1970 O—356-352